

# INSECTES SOCIAUX

BULLETIN DE L'UNION INTERNATIONALE POUR L'ÉTUDE DES INSECTES SOCIAUX



UNIVERSITY OF HAWAII  
LIBRARY  
DEC 30 '58

## COMITÉ DE RÉDACTION

J. D. CARTHY, P. H. CHRISTENSEN, A. C. COLE,  
K. GÖSSWALD, P.-P. GRASSÉ, C. JUCCI,  
A. RAIGNIER, D. STEINBERG, T. UCHIDA

---

**Volume V - Octobre 1958 - Numéro 3**

MASSON & C<sup>ie</sup> ÉDITEURS - PARIS

PUBLICATION PÉRIODIQUE TRIMESTRIELLE.



## INSECTES SOCIAUX

---

Revue consacrée à l'étude de la Morphologie, de la Systématique et de la Biologie des Insectes sociaux.

*Publiée sous les auspices de*

**L'UNION INTERNATIONALE POUR L'ÉTUDE DES INSECTES SOCIAUX**

---

### COMITÉ DE RÉDACTION

- J. D. CATHY, Department of Zoology, Queen Mary College, Mile end Road, London E1 (England).
- P. H. CHRISTENSEN, Universitetets Institut for almindelig Zoologi, Universitetsparken 3, Copenhagen, Denmark.
- A. C. COLE, Department of Zoology and Entomology University of Tennessee, Knoxville, Tennessee (U. S. A.).
- K. GÖSSWALD, Institut für Angewandte Zoologie der Universität Würzburg, Röntgenring 10, Würzburg, Deutschland.
- P.-P. GRASSÉ, Laboratoire d'Évolution des Êtres organisés, 105, boulevard Raspail, Paris-VI<sup>e</sup>, France.
- C. JUCCI, Istituto di Zoologia « L. Spallanzani », Pavia, Italia.
- A. RAIGNIER, 11, rue des Récollets, Louvain, Belgique.
- D. STEINBERG, Zoological Institute, Academy of Sciences of the U. S. S. R. Leningrad 164, U. S. S. R.
- T. UCHIDA, Zoological Institut Faculty of Sciences, Hokkaido University Sapporo, Japan.

---

### PRIX DE L'ABONNEMENT POUR 1958

France et Union Française : **3 000 frs.**

Étranger { Dollars U. S. A. : **9,25.**  
              { Francs Belges : **460.**

Également payable au cours officiel  
dans les autres monnaies.

Prix spécial pour les membres de l'Union internationale pour l'étude des Insectes sociaux.

France et Union Française : **2 000 frs.**

Étranger { Dollars : **5,75.**  
              { Francs Belges : **286.**

Règlement : a) Chèque sur Paris d'une banque officielle.  
              b) Virement par banque sur compte étranger.  
              c) Mandat International.

### ADMINISTRATION

---

MASSON et C<sup>ie</sup>, Éditeurs

120, boulevard Saint-Germain, PARIS-VI<sup>e</sup>

o o

### SECRÉTAIRE

---

M. G. RICHARD

105, Boulevard Raspail, PARIS-VI<sup>e</sup>

# INSECTES SOCIAUX

BULLETIN DE L'UNION INTERNATIONALE  
POUR L'ÉTUDE DES INSECTES SOCIAUX

---



## SOMMAIRE

---

### *Mémoires originaux.*

An analysis of polymorphism in social Wasps, by R. E. BLACKITH.....	263
Le comportement de construction chez <i>Formica rufa</i> I, par Rémy CHAUVIN..	273
The relation of stridulation behaviour to ecology in certain Grasshoppers, by P. T. HASKELL.....	287
Études sur les Formicidæ. IV. Sur le venin du Dolichodéride <i>Tapinoma niger- rimum</i> Nyl, par M. PAVAN et R. TRAVE.....	299
Interattraction olfactive chez <i>Calotermes flavicollis</i> . II. Pouvoir attractif des nymphes à l'égard des différentes castes, par Henri VERRON.....	309
Polyethism in workers of the Ant <i>Myrmica</i> (Part II), by J. S. WEIR.....	315

### *Nouvelles de l'union.*

Communiqué .....	343
Modification à la liste des membres.....	343
Compte rendu de la réunion de la Section française.....	343

---

# INSECTES SOCIAUX

BULLETIN DE L'UNION INTERNATIONALE  
POUR L'ÉTUDE DES INSECTES SOCIAUX

---

*Comité de Rédaction :*

J. D. CARTHY, P. H. CHRISTENSEN, A. C. COLE,  
K. GÖSSWALD, P.-P. GRASSÉ, C. JUCCI,  
A. RAIGNIER, D. STEINBERG, T. UCHIDA

---

TOME V

N° 3

MASSON & C<sup>ie</sup>, ÉDITEURS  
120, boulevard Saint-Germain, PARIS-VI<sup>e</sup>

---

1958

---



# AN ANALYSIS OF POLYMORPHISM IN SOCIAL WASPS

by R. E. BLACKITH

(Imperial College Field Station, Sunninghill, Berks.)

## INTRODUCTION

This paper describes the differences of form between adult queens, males and workers of three species of social wasp: *Vespula germanica* Fabr., *V. rufa* L and *V. vulgaris* L. Recent developments in morphometric analysis permit distinctions to be drawn between several fundamentally different modes of growth in insects and enable us to discover how many of these different modes have been elicited in the immature stages, ultimately influencing the form of the adult integument. Moreover, it is often possible to identify these underlying growth processes by comparing the shapes and sizes of related groups of insects in terms of those linear vectors (discriminant functions and their associated generalised distances) which provide a quantitative mathematical description of changes of growth and form. This investigation is intended to throw some light on the differences between queen and worker wasps, whether this difference is solely one of size, or whether caste formation is associated with distinct changes of shape as well.

## MATERIAL AND METHODS OF MEASUREMENT

As WRIGHT, LEE and PEARSON (1907) have noted, social wasps are excellent material for morphometric analyses, being amongst the most homogeneous of all animals. These authors measured the forewings of 129 queens, 130 males and 129 workers of *V. vulgaris* and their data have been used in that part of this paper which is concerned with the shape of wings; otherwise, seven characters have been measured on the 306 queens, males and workers of the other two species taken from nests at this Field Station some 30 km. west of London. The numbers of insects measured in each group, and the mean values of the various measurements, are set out in Table I.

Some of the characters were chosen for their accessibility to the new direct-reading caliper gauges described by BLACKITH, VERDIER and ALBRECHT (1958). The use of the reduced weight of the insects as a morphometric character, which estimates the size in terms of the dry weight of the head and thorax and appendages, has also been described by these authors, who note that it avoids the vagaries of the wet weights of the digestive and reproductive systems. The number of hamuli, and also the abdominal width at the first apparent tergite (the second true abdominal tergite) have been found useful components of the discriminant functions used by RICHARDS and RICHARDS (1951) to distinguish two types of female in the South American species *Apoica pallens* Fabr.

The 100 workers of *V. germanica* were divided into two groups according to their reduced weight. Those weighing more than 17.8 mg. were classified as "large" workers, those below this level as "small" workers. The weight chosen is very close to the mean for the entire sample, and equal numbers of wasps fell into either group. This equality suggests an initially symmetrical, rather than a log. normal, distribution



of reduced weights. Symmetry of the wing-lengths (WRIGHT, LEE and PEARSON, 1907) and of eyelengths (BLACKITH, 1958) as distributions has already been recorded in the literature. The logarithmic transformation was therefore withheld from the data prior to analysis. Moreover, the small workers were more variable than the large workers in respect of each of the seven characters, an unusual situation since the variance of a morphometric character tends to increase with the size of the organism. Thus the application of the logarithmic transformation would have secured neither symmetrical distributions nor stabilised variances. The advantages of being able to contrast large and small workers of one species seemed to outweigh the disadvantages, probably not very serious, of truncating the distributions of the characters of the *germanica* workers. However, where workers of this species are contrasted with other groups as a whole, the statistics proper to the entire group are given.

The sexual dimorphism, and the specific distinctions, have been studied to provide a framework of reference within which may be set the differences between castes. For if caste determination is no more than a matter of reduced growth on an inferior diet, one might expect the workers to have the same form as the queens, but diminished in size isometrically. However, WRIGHT, LEE and PEARSON (1907) have said of *V. vulgaris* that "while the drone's and queen's wings are roughly magnifications of that of the worker, they are not exact replicas on an enlarged scale, but are distorted in different manners". Experience with locusts and grasshoppers suggested that such distortions offered promising opportunities for the assessment of the biological basis of polymorphism (BLACKITH, 1957).

## METHODS OF ANALYSIS

Allometric modes of growth may be compared in terms of the different morphometric characters compounded into those discriminant functions which best separate the polymorphic forms to which the allometric growth gives rise. These discriminant functions consist of the weighted sums and differences of the characters, the weights being so calculated as to ensure the greatest possible separation between the different groups of organism. The actual separation afforded in any particular comparison is known as the generalised distance between the groups. Moreover, this separation takes place in a definite direction, as well as to a calculable extent, as a consequence of the vector properties of the discriminant function. Thus the shapes of male wasps will best be distinguished from that of females by the function  $2.34$  (wing-length)  $+12.88$  (wing-breadth)  $+2.95$  (No. of hamuli)  $+11.29$  (abdominal width)  $+17.95$  (thoracic width)  $+13.74$  (head-width)  $+0.46$  (reduced weight). The quite different set of weights:  $-3.11$ ;  $-38.13$ ;  $-1.79$ ;  $20.39$ ;  $11.92$ ;  $31.23$ ;  $-0.40$  is the most effective in separating the shapes of *germanica* and *rufa* queens.

The calculation of these weights and of the amount of separation they afford is described by RAO (1952) and by BLACKITH (1957). Both these authors have described the construction of charts in which all the various groups of organisms are arranged so that the appropriate generalized distance lies between each pair of groups. Theoretically, the space occupied by the framework of generalised distances arranged in this way may have as many dimensions as there are measured characters. However, in practice, there are unlikely to be more than a few dimensions, since each one must correspond to a different mode of growth in the insect. Only with exopterygotous insects can these modes of growth be traced through the immature stages, with rare exceptions.

According to the number of these basic growth patterns the adult forms may be arranged in a space of some few dimensions. Thus, if wasps of the genus *Vespula* differed in size but not in shape, the different groups could be arranged on a straight line. If one basic difference of shape is present in addition to that of size then a planar chart is required. A solid model, or its projection, will be needed to represent the groups if more than one distinction of shape is met with, as well as that of size variation.



This dimensionality of the chart is, in any practical application of the method, determined by inspection of the model or of its projections. Should the number of dimensions appear to exceed three, or the existence of some minor source of variation require confirmation, the calculation may be arranged so as to provide objective tests of the dimensionality (RAO, 1952).

## RESULTS AND DISCUSSION

Before turning to the results of the main analysis, we may note some special relationships between the characters. That between the length and width of the wings is unusually close to isometry, although WRIGHT, LEE and PEARSON (1907) found that some degree of allometry could be detected between the wing dimensions of *V. vulgaris*, including internal cell dimensions. The correlation between the two characters as between groups is unusually high compared with that within groups (between groups;  $r = 0.991$ , 4 d.f.: within groups;  $r = 0.62$ , 299 d.f.). These coefficients are calculated for *rufa* and *germanica* only; WRIGHT, LEE and PEARSON showed how variable could be the correlations within groups, for *vulgaris* their values are 0.91 for the workers, 0.77 for the males, and 0.60 for the queens. The high value for workers doubtless reflects the wide range of sizes of this caste.

Differential variability of the groups of wasp is of interest because the suggestion has been made that insects produced parthenogenetically might be more homogeneous than biparental forms. CASTEEL and PHILLIPS (1903) showed that the wings of worker honey-bees were less variable than those of the males. However, WRIGHT, LEE and PEARSON found that the reverse obtained in *V. vulgaris*. In fact, any putative reduction of variability in male wasps accompanying parthenogenesis is masked by the large specific differences in variability. For instance, the workers of *V. germanica* are significantly more variable than the males in respect of the width of head and of wing; whereas in *V. rufa* the workers are significantly the more homogeneous in respect of all the seven characters. This marked reversal as between similar species of a genus is shown to be essentially a matter of differential male, rather than of worker, variability by the fact that the *rufa* males are significantly more variable than those of *germanica* in four of the seven characters (widths of wing, of abdomen, and of thorax, and no. of hamuli).

Since all the insects of one species were taken from a single nest, the cause of this differential variation is obscure. THOMPSON, BELL and PEARSON (1910) found that there was a twofold increase in variability when insects were taken from several nests and compared with a single nest population. Moreover, the extent of the queen wing-length/worker wing-length dimorphism in *Vespula* seems to differ as much from nest to nest as from species to species. A ratio of 1.27 was obtained by WRIGHT, LEE and PEARSON (1907) for one nest of *V. vulgaris*, whereas RICHARDS (1949) found a nest with longer queen wings and shorter worker

wings than those earlier measured, the caste dimorphism being 1.39. TAKAMATSU (1951) measured 190 queens and 825 workers of *V. lewisii* (Cameron) from a single nest, the ratio of wing-lengths being I.II; in Table I the ratio for *V. germanica* works out at 1.27, that for *V. rufa* at 1.32. Mean wing lengths for workers of different species range from 9.82 to 10.74 mm., but the queens vary over more than twice this range, 11.61 to 13.81 mm. which does not suggest undue worker variability as a disturbing factor.

TABLE I. — MEAN VALUES OF MORPHOMETRIC CHARACTERS FOR TWO SPECIES OF WASP.

Number measured. CHARACTER.	<i>V. germanica.</i>			
	Queens 15	Males 50	Workers (large) 50	Workers (small) 50
Length of wing (mm.)	13.8133	12.4070	11.2480	10.4580
Breadth of wing (mm.)	4.1800	3.8340	3.5700	3.3010
No. of hamuli	29.8000	24.7400	27.1000	25.3000
Width of abdomen (mm.)	5.6547	4.0080	4.0160	3.8090
Width of thorax (mm.)	5.2267	3.8210	3.9400	3.6768
Width of head (mm.)	4.5840	3.6306	3.8974	3.6696
Reduced weight (mg.)	43.9866	19.7920	20.4560	15.2060

Number measured. CHARACTER.	<i>V. rufa.</i>		
	Queens 49	Males 42	Workers 50
Length of wing (mm.)	12.9929	11.4286	9.8170
Breadth of wing (mm.)	4.0653	3.4905	3.1270
No. of hamuli	34.7143	27.3809	26.7000
Width of abdomen (mm.)	4.9071	3.7417	3.6536
Width of thorax (mm.)	4.7978	3.5933	3.5942
Width of head (mm.)	4.2565	3.3638	3.5594
Reduced weight (mg.)	38.4755	16.8547	15.0920

The measurements of the numbers of hamuli (Table I) generalise those made by RICHARDS (1949), on *V. vulgaris*, for which species the number of hamuli, wing-length, and weight were correlated significantly. When the mutual dependence on wing-length was eliminated, the weight and number of hamuli were no longer related. In the present work, the pooled total correlation between reduced weight and no. of hamuli for *V. rufa* and *V. germanica* is 0.117, not significantly different from zero, when based on 299 d.f. even before the influence of wing-length was eliminated.

The no. of hamuli per unit length of wing was found by RICHARDS to decrease for longer wings, both within a series of *vulgaris* workers and as between workers and queens. In *germanica* the density of hamuli is 2.16 for



queens, 2.41 for workers of the "large" group and 2.42 for "small" workers, distinctly higher than RICHARDS' values for comparable *vulgaris* groups, for which the densities are 1.96; 2.16; and 2.34. *V. rufa* has 2.67 hamuli per mm. for queens, and 2.72 for workers. This specific difference is also found in the males, being 1.98 for those of *germanica* and 2.39 for those of *rufo*. The hypothesis that the number of hamuli per unit wing-length is associated with the need to forage is supported by the consistently higher density on worker wings, compared with those of queens, and on the wings of either female caste compared with males of its own species. Nevertheless, the extent to which this putative response to foraging requirements is overlaid by the specific distinctions is apparent from the

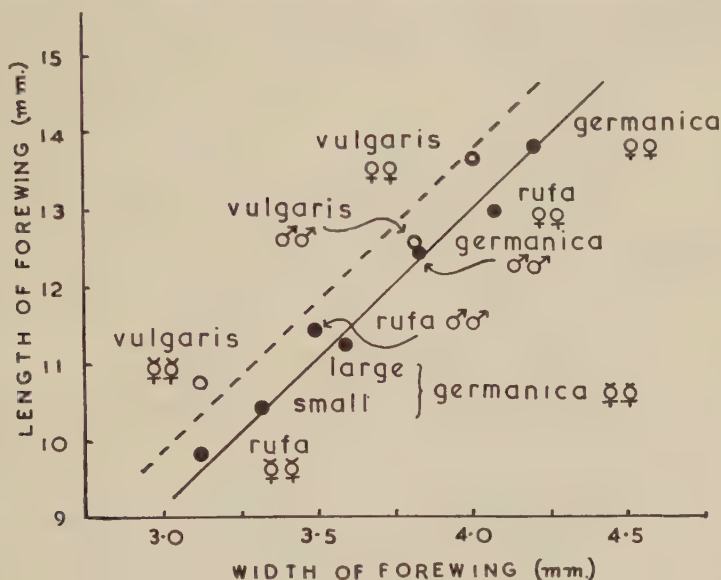


FIG. 1. — Isometric relationship between dimensions of forewings of *Vespa* spp.

fact that *rufo* males have almost as dense hamuli as have *vulgaris* workers.

The number of hamuli is more closely related to the length of the wing ( $r = 0.54$ ) than to the breadth ( $r = 0.36$ ) for *germanica* and *rufo* of all groups.

The virtual isometry of the wing lengths and breadths seems unlikely to be required on aerodynamic grounds, since the *rufo* wings seem to be much smaller, group for group, than the relative weights of the different species might suggest. There is some evidence that the *vulgaris* wings are longer for their breadth than the wings of the other two species (fig. 1). The instructions for measuring wings given by WRIGHT, LEE and PEARSON (1907) are explicit and have been closely followed to ensure comparability, when the other species were considered. The relations between wing length and body weight have also been studied by TAKAMATSU (1951).

Although the thoracic width is much the same for males as for workers

in *V. rufa* and *V. germanica*, the heads of the males are narrower, and their abdomens broader, than those of the workers of the same species (Table I).

TABLE II. — THE 21 GENERALISED DISTANCES BETWEEN THE DIFFERENT GROUPS OF WASPS.

<i>V. germanica.</i>	Males	<i>V. germanica.</i>		
		Queens	Workers (large)	Workers (small)
Males .....	0	13.32	6.60	6.57
Queens .....		0	10.57	12.01
Workers (large) .....			0	3.05
Workers (small) .....				0

<i>V. germanica.</i>	<i>V. rufa.</i>		
	Males	Queens	Workers
Males .....	4.43	11.01	7.95
Queens .....	14.37	5.95	12.39
Workers (large) .....	8.09	8.12	4.68
Workers (small) .....	6.80	12.59	2.30

<i>V. rufa.</i>			
Males .....	0	11.29	6.89
Queens .....		0	9.96
Workers .....			0

This dimorphism recalls that found by BRIAN (1954) to exist between male and female larvae of the ant *Myrmica rubra* L. Probably the adult form reflects larval polymorphism. The virgin queens (gynes) of the wasps exhibit a more disproportionate expansion posteriorly than either males or, of more importance, than workers. The allometric indices, in Table III, relate to the same character measured in two different groups

TABLE III. — ALLOMETRIC INDICES FOR BODY-MEASUREMENTS OF « VESPULA » SPP.

Queen-worker comparisons.		
CHARACTER	<i>V. germanica.</i>	<i>V. rufa.</i>
Width of head .....	1.218	1.196
Width of thorax .....	1.372	1.335
Width of abdomen .....	1.445	1.343

Queen-male comparisons.		
CHARACTER.	<i>V. germanica.</i>	<i>V. rufa.</i>
Width of head .....	1.263	1.265
Width of thorax .....	1.368	1.335
Width of abdomen .....	1.411	1.312



of insects, rather than to different characters measured on one group, as is more common. The steady progression of the indices posteriorly demonstrates conclusively that the workers differ from the queens in shape as well as size. To examine this difference of form more closely we need to employ methods of multivariate analysis.

*The generalised distance chart.*

When all the generalised distances between the groups had been calculated, the model was realised geometrically in the form of fig. 2. This chart is undoubtedly at least three-dimensional, so that projections are given from two aspects. Since the solid model did not unite the

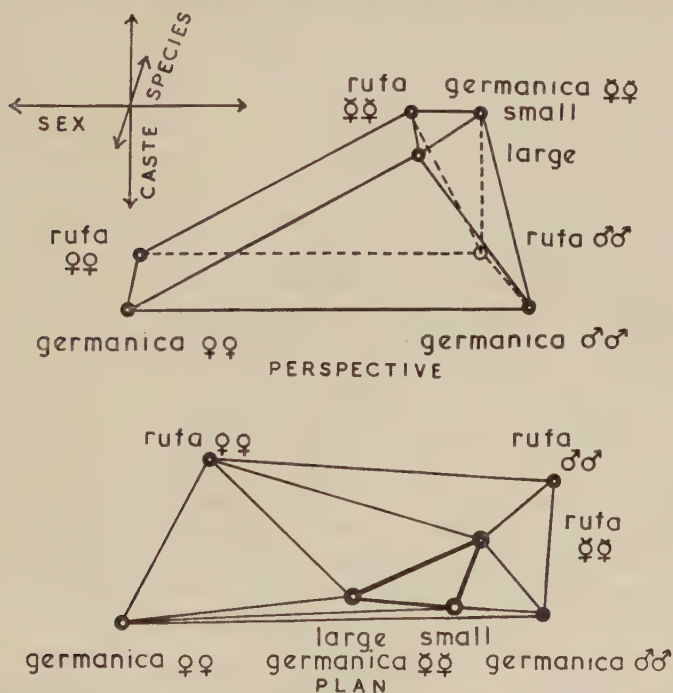


FIG. 2. — Three-dimensional generalised distance chart based on 7 morphometric characters.

several generalised distances with the accuracy previously experienced in work on Acrididæ, a fourth dimension, accounting for some small fraction of the total variation, may exist. Nevertheless, such a dimension would be hard to identify on the available evidence, and attention will be concentrated on the three most important dimensions.

The largest source of variation of form is evidently the sexual dimorphism between the queens, all found at one end of the chart, and the males at the other. The second main dimension is that between the

structural types of the two species. The structural type represents the average shape and size of individuals within a definable homogeneous group, particularly within a species (COUSIN, 1948).

The three generalised interspecific distances, lying respectively between the queens, the males and the workers, are each aligned almost at right angles to the vectors which link the different forms within a species. We should expect specific differences to be independent of the sexual dimorphism, and the chart confirms this expectation.

Finally, a third dimension of variation comprises the general distinction between the sexual forms and the workers. Caste formation is evidently not just a matter of size changes, but involves a radical modification of form as between queens and workers, as the preliminary analysis suggested, though the process also involves a substantial size change as well. The workers occupy a position on the general size dimension, which we may roughly equate with the sexual dimorphism dimension, intermediate between the queens and males, but lying in a different plane. The large *germanica* workers are noticeably less distinct from the queens than are the small workers, not only in size, as should obviously be the case, but in caste status as measured by the dimension at right angles to the size and specific dimensions. In all probability, for a genus in which the queens and workers are less clearly differentiated than they are in *Vespula*, the queens and workers would intergrade along the line which, in the generalised distance chart of fig. 2, links the two castes. Such a situation strongly suggests that even in *Vespula* the formation of castes is determined quantitatively rather than qualitatively, although it may be that some quantitative factor such as diet moderates a dimorphism which is earlier established. It was, however, EZHIKOV'S (1934) view that quantitative influences such as diet, crowding and parasitism could stimulate the several modes of growth in social insects to different extents, producing just such a situation as that outlined here. The differential stimulation, or inhibition, of distinct modes of growth is well known to occur in insects, particularly in those Acrididæ which show phase variation, and may include differential modification of modes of growth partly under genetic control.

### Summary.

The polymorphism of social wasps has been studied by arranging the different structural types in a generalised distance chart. These structural types group the wasps according to their sex, caste and species. Between each of a pair of types is the appropriate generalised distance, that is, the vector separation afforded by seven morphometric characters, combined into a discriminant function. The mutual orientation of these generalised distances reflects the various underlying modes of growth elicited during the larval instars, when all the distances are put together in a chart.



The dimensionality of this chart thus suggests the number of modes of growth to be considered, and in these wasps there seem to be not more than three important sources of variation. These sources are the sexual dimorphism, the specific polymorphism, and a dimension which expresses the caste status of the insects. Larger workers resemble the queens more than do smaller workers not only in size but also in respect of their caste status. This greater resemblance suggests the influence of a quantitative factor in caste determination.

The external wing dimensions of wasps are almost isometric, but the width of the body expands posteriorly far more in the queens than it does in the workers, even taking into account their different sizes: such a relation is allometric.

If their parthenogenetic origin confers any greater uniformity on the males, this enhanced homogeneity of form is masked by the substantial specific differences in male variability as compared with that of the workers.

### *Sommaire.*

Dans le but d'éclaircir le polymorphisme des Guêpes sociales on a construit un diagramme qui fait ressortir les relations entre les divers types structuraux. Ces types structuraux groupent les guêpes selon leur sexe, leur caste et leur espèce. Chaque paire de types possède sa propre distance généralisée, c'est-à-dire la séparation vectorielle produite par sept caractères morphométriques combinés dans une fonction discriminative. L'orientation mutuelle des écartements associés aux distances généralisées nous permet de distinguer, dans ces Guêpes, les diverses façons de se développer pendant les stades larvaires.

La dimensionalité du modèle représentant le diagramme des distances généralisées laisse entrevoir qu'il n'y a que trois sources importantes de variation qui sont : le dimorphisme sexuel, le polymorphisme entre espèces voisines, et une dimension qui exprime l'état de caste des insectes. Il paraît que les grandes ouvrières s'approchent des reines plus que les petites ouvrières, non seulement par rapport à la taille, mais aussi à l'égard de leur état de caste. Cette ressemblance plus proche nous fait soupçonner l'influence d'un facteur quantitatif de détermination de caste.

Les dimensions externes des ailes des Guêpes sont presque isométriques, mais la largeur du corps s'étend postérieurement bien plus chez les reines que chez les ouvrières, même en tenant compte de leur différence de taille ; cette relation est allométrique.

Si l'origine parthénogénétique confère aux mâles une uniformité de forme plus grande, celle-ci est masquée par des différences spécifiques considérables dans la variabilité des mâles par rapport à celle des ouvrières.

*Epitome.*

Vespæ sociales formarum conferendarum causa generatim disponuntur. Diversitates inter binas formas, quæ ex septem proprietatibus vesparum oriuntur, ita expromuntur ut varii immaturarum crescendi modi appareant. Hinc tres formarum variantium causas, sexum, gentem, ordinem dignoscimus.

Maiores operantes reginis similiores sunt quam minores, non solum quod ad magnitudinem sed etiam quod ad ordinem attinet; refert ad rem quæ ordinem constituit quam medii gradus reperiri. Mensuræ exteræ alæ pro rata stant, latitudo autem corporis plus etiam reginis quam operantibus retroversum patet, verum enimvero plus quam pro amplitudinibus propriis.

Si mares quopiam modo natum propter parthenogeneticum æquabiliores fiunt, non apparet hæc emendatio in formis, quippe quæ plus quam reginarum variant.

## REFERENCES

1957. BLACKITH (R. E.). — Polymorphism in some Australian locusts and grasshoppers (*Biometrics*, **13**, 183-196). — 1958. Foraging and visual sensitivity in social wasps (*Insectes Sociaux*, **5**, 159-169).
1958. BLACKITH (R. E.), VERDIER (M.), ALBRECHT (F.-O.). — Quelques nouvelles techniques utilisables en analyse morphométrique (*In preparation*).
1954. BRIAN (M. V.). — Studies of caste differentiation in *Myrmica rubra* L. I. The growth of queens and males (*Insectes Sociaux*, **1**, 101-122).
1903. CASTEEL (D. B.), PHILLIPS (E. F.). — Comparative variability of drones and workers of the honey-bee (*Biol. Bull.*, **6**, 18-37).
1948. COUSIN (G.). — Hybridations interspécifiques et transmission des types structuraux (*Bull. Biol. Fr.-Belge*, **82**, 331-387).
1934. EZHIKOV (T.). — Individual variability and dimorphism of social insects (*Amer. Nat.*, **68**, 333-344).
1952. RAO (C. R.). — *Advanced statistical methods in biometric research* (Wiley, New York).
1949. RICHARDS (O. W.). — The significance of the number of winghooks in bees and wasps (*Proc. R. ent. Soc. Lond.*, **24**, 75-78).
1951. RICHARDS (O. W.), RICHARDS (M. J.). — Observations on the social wasps of South America (Hymenoptera Vespidae) (*Trans. R. ent. Soc. Lond.*, **102**, 1-170).
1951. TAKAMATSU (Y.). — Studies on *Vespula lewisii* (Cameron), IV. On the quantitative relations, with reference to sex, between the length and weight of the body and the length of the wing in all the members constituting one nest (*Physiol. Ecol.*, **4**, 102-104).
1910. THOMSON (E. Y.), BELL (J.), PEARSON (K.). — A second cooperative study of *Vespa vulgaris*. A comparison of the queens of a single nest with queens of a general population (*Biometrika*, **7**, 48-63).
1907. WRIGHT (A.), LEE (A.), PEARSON (K.). — A cooperative study of queens, drones and workers in *Vespa vulgaris* (*Biometrika*, **5**, 407-422).



## LE COMPORTEMENT DE CONSTRUCTION CHEZ *FORMICA RUFA*

par

Rémy CHAUVIN

(Station de Bures-sur-Yvette, Laboratoire d'Ethologie, Seine-et-Oise).

Le dôme de brindilles de *Formica rufa* constitue un des objets les plus communs des forêts d'Europe occidentale, mais il n'a été l'objet que d'expériences et d'observations assez peu nombreuses. Nous avons des renseignements sur les échanges de température en son intérieur (STEINER). Plus récemment, KLOFT, en teignant les matériaux superficiels du nid d'une couleur aisée à reconnaître, a pu remarquer une « cyclose » à la surface de la construction. : les matériaux colorés sont d'abord couverts de brindilles, puis, au bout d'un temps plus ou moins long, reparaissent à la surface. D'autre part, les très belles études de GÖSSWALD ne portent qu'en partie sur le nid.

Celui-ci est pourtant remarquable par plusieurs caractères si évidents que l'observateur oublie de s'en étonner. D'abord, il *s'agit d'un dôme* très régulier quand il est suffisamment âgé et volumineux, et que des obstacles mécaniques ne s'opposent point à l'arrondi de ses contours ; ensuite, sa *surface est propre* ; par exemple, on n'y voit presque jamais de feuilles mortes, bien que les *Formica* nidifient sous bois. Et c'est même à la régularité de la forme et à la netteté de la structure que l'on reconnaît de loin les dômes des Fourmis. Mais quels sont les facteurs qui gouvernent forme et structure ? Voilà ce que n'apprend point jusqu'à présent, me semble-t-il, la lecture des travaux des myrmécologues. C'est donc à cette étude que je me suis attaché pendant le printemps, l'été et l'automne de 1957. Douze fourmilières d'un bois situé près d'Épernon (Eure-et-Loir) ont été suivies assidûment et les résultats obtenus posent des problèmes complexes.

### *Les facteurs microclimatiques et les fourmilières.*

Il m'a semblé important de rechercher d'abord si éclaircissement, hygrométrie ou température ne pouvaient agir sur les fourmilières. A vrai dire, cela semble peu probable, car on en trouve à des expositions très différentes, allant du plein soleil à l'ombre épaisse des sous-bois, et leur morphologie externe tout au moins ne paraît pas s'en ressentir. J'ai

tenté cependant de modifier fortement les facteurs microclimatiques. J'ai d'abord recouvert une fourmilière en voie de développement rapide de plusieurs épaisseurs d'un papier opaque soulevé par des piquets et qui ne se trouvait pas en contact immédiat avec le dôme. Le papier retom-

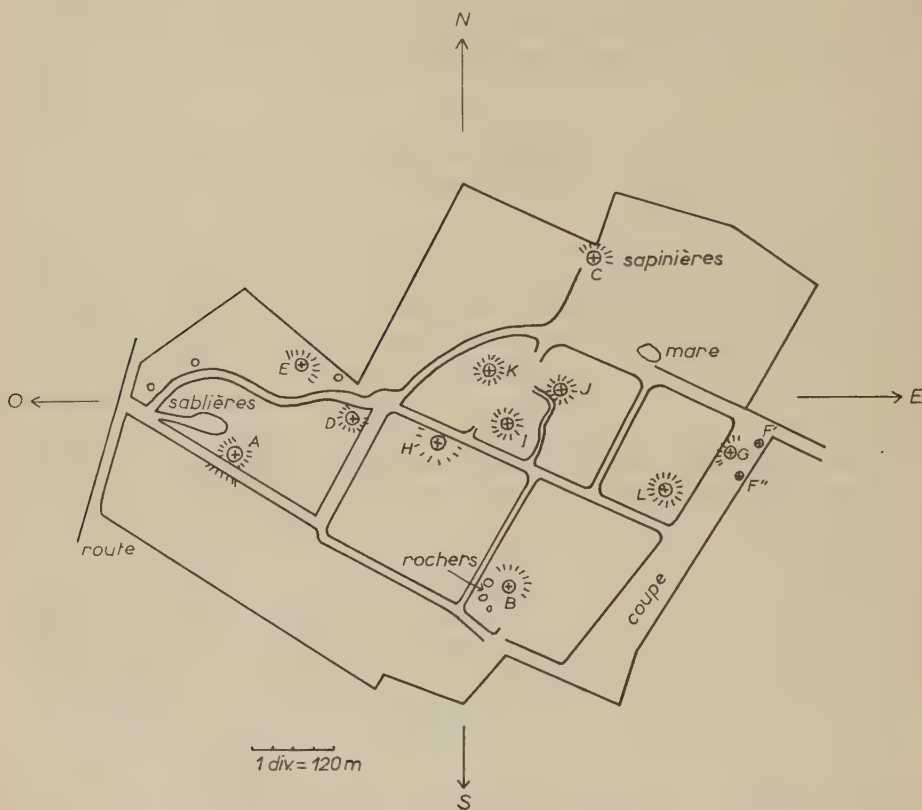


FIG. 1. — Plan du bois et des sentiers le long desquels se trouvent les fourmilières étudiées. Les fourmilières sont représentées par des cercles avec une croix inscrite. Le cercle de tirets, complet ou réduit à sa moitié, correspond aux ombrages qui entourent le nid plus ou moins complètement.

bait jusqu'à terre afin d'empêcher le plus possible l'entrée des rayons lumineux.

L'*hygrométrie* a été fortement modifiée dans deux autres fourmilières en suspendant au-dessus d'elles deux récipients d'une dizaine de litres dont l'eau s'échappait goutte à goutte et tombait au milieu du nid. Enfin, j'ai tenté de modifier la *température*, en même temps que l'équilibre des radiations, en enfermant en partie une quatrième fourmilière sous une cage vitrée. Dans aucun cas, et bien que les expériences aient duré fort longtemps (quinze jours à un mois) il ne m'a été possible de déceler une influence quelconque de ces importantes modifications des agents externes sur la morphologie ou le développement du nid. Songeant à l'extrême varia-

bilité des expositions signalée plus haut, je n'ai pas poussé plus loin dans cette voie.

Je pense donc qu'il faut admettre, au moins provisoirement, que la structure ni la forme du nid ne dépendent guère des agents externes chez *Formica rufa*. L'activité des déplacements est réglée toutefois par les conditions météorologiques, c'est bien évident ; mais, comme nous le verrons plus loin, elle n'est pas forcément reliée d'une manière simple à l'activité de construction.

### *Le nettoyage du Nid.*

Comme je le disais un peu plus haut, une des raisons pour lesquelles on remarque de loin le nid des Fourmis est la propreté du dôme. Pourtant des feuilles et des brindilles y tombent certainement, à partir des arbres qui surplombent la fourmilière : les Fourmis doivent donc s'en débarrasser de quelque manière.

Il est aisé de vérifier qu'elles le font effectivement en plaçant sur le dôme des feuilles vertes ou mortes et des débris divers. On peut observer alors trois types de comportement :

a) Si l'on dépose un objet *filamenteux* de diamètre variable (depuis le fil à coudre jusqu'à la ficelle de 1 mm de diamètre, sur 1 m de long), les Fourmis ne paraissent pas s'en soucier, mais le recouvrent rapidement de brindilles.

b) S'il s'agit de feuilles mortes de grande taille et qu'elles se trouvent sur la pente du dôme, elles sont tirées et poussées apparemment au hasard et finissent par glisser jusqu'en bas. Si elles se trouvent, au contraire, sur le sommet et que les ouvrières ne puissent les remuer, elles les couvrent de brindilles.

c) Des solides prismatiques ou de formes variées sont recouverts suivant la même technique. Les Fourmis peuvent y grimper, mais elles ne le font pas d'habitude : elles se contentent d'amasser des brindilles à leur base. Si le solide présente une surface plane supérieure, elles n'y déposent presque rien. Lorsqu'une plaque de verre de grande taille recouvre toute la colonie, ou bien elle est laissée intacte si la force de la colonie n'est pas très grande, ou bien elle est recouverte, mais au bout d'un temps très long.

d) Mais le comportement le plus intéressant s'observe dans le cas de brindilles de la taille d'une allumette, c'est-à-dire de dimensions assez voisines des matériaux qu'emploient habituellement les Fourmis. Lorsque les allumettes sont simplement posées sur le nid, elles sont presque immédiatement transportées jusqu'à la base ; une ou deux ouvrières suffisent à cette tâche. J'ai essayé de rechercher des différences possibles dans l'activité de nettoyage en disposant des allumettes en cercles concentriques, et en les photographiant à intervalles réguliers ; mais je ne suis arrivé à rien de précis jusqu'à présent ; en tout cas, l'ordonnance des cercles est très rapidement et irrégulièrement dérangée.



Les phénomènes sont peut-être plus nets en enfonçant dans les brindilles du dôme des allumettes jusqu'à la moitié de leur longueur. Elles sont très rapidement arrachées par une ou deux Fourmis, parfois trois, et rejetées jusqu'à la base du nid ; il arrive même qu'elles soient transportées au-delà, jusqu'à une dizaine de centimètres plus loin.

Si les circonstances atmosphériques sont favorables, une couronne de 7 à 8 cm de diamètre, formée d'allumettes implantées au sommet du dôme, est arrachée en trois à quatre heures. Lorsque les allumettes sont attachées par un fil à un poteau central, les Fourmis tirent sur elles pendant des heures et des journées entières, mais ne coupent pas le fil ; alors qu'elles le coupent assez vite si une proie comme une Guêpe morte, et non plus une brindille, lui est attachée. Lorsqu'on replante pendant quatre ou cinq jours de suite les allumettes arrachées dans la même fourmilière, les Fourmis finissent par les laisser et les recouvrir de brindilles. Sans doute assistons-nous alors à une *familiarisation* comparable à ce qu'on voit pendant la phase d'exploration des proies chez les mêmes Fourmis (CHAUVIN). Mais une telle hypothèse pose encore des problèmes, car les allumettes sont rejetées pendant un temps vraiment fort long, avant que les Fourmis ne se décident à les accepter ; alors que l'acceptation est beaucoup plus rapide dans le cas des proies. Sans doute les nombreux traitements chimiques auxquels est soumise l'allumette sont-ils en partie responsables de cette répugnance.

Ce nettoyage du dôme implique un certain degré de coordination, qui va beaucoup plus loin lorsqu'on plante des baguettes de 20-25 cm et 3-4 mm de diamètre, enfoncées jusqu'à la moitié de leur longueur. Au bout d'un long délai (trois à quatre semaines), on constate qu'elles s'inclinent fortement. Si leur base est seulement fixée dans la souche très vermoulue qui forme le centre de la fourmilière ou, mieux encore, dans les brindilles, il arrive qu'elles se couchent complètement et soient intégralement recouvertes. Le processus est très lent et je n'ai pu l'étudier en détail. Il s'agit, semble-t-il, d'un remaniement progressif du dôme, entrepris dans les heures qui suivent sa pose tout autour de sa base, mais poursuivi ultérieurement d'un seul côté. Alors, la baguette s'incline et les Fourmis continuent à affouiller le dôme en dessous, ce qui l'amène plus ou moins tôt dans le plan horizontal. J'insiste sur le fait que le phénomène n'est pas rare, bien qu'il ne se produise pas dans tous les cas ; et il est à peine besoin de noter l'étonnante coordination qu'il pourrait impliquer.

### *Les changements dans les matériaux de construction.*

Il est possible d'enlever complètement les brindilles et de les remplacer par d'autres matériaux. Le trouble n'est pas aussi profond qu'on pourrait croire, car il ne touche guère une grande partie de la population de la fourmilière tapie profondément dans les anfractuosités de la souche centrale.

J'ai substitué à ces brindilles de la sciure de bois, des pommes de sapin, du foin ou des feuilles mortes. Le volume de tous ces matériaux était approximativement équivalent à la moitié de celui de la fourmilière.

Quelques heures après, les Fourmis manifestent une agitation énorme, mais qui paraît diffuse, en ce sens qu'on ne voit pas tout de suite d'apport de brindilles ; il ne débute que le lendemain de l'opération. La sciure de bois n'est pas colonisée ; d'ailleurs, les Fourmis n'arrivent qu'avec peine à l'escalader et glissent à de nombreuses reprises sur la pente du tas. Au bout de deux à trois jours cependant, elle est totalement recouverte de brindilles et, à partir de là, la construction progresse normalement. Le tas de pommes de pin est adopté immédiatement. La perturbation est plus forte dans le cas du foin, et la colonisation demande huit jours au moins pour faire de sérieux progrès. La colonie très forte et très active, où j'avais substitué le foin aux brindilles, a même émigré en partie dans cinq souches de sapin vermoulues situées à 1-2 m de la fourmilière. Mais, dès que les brindilles ont commencé à réapparaître au-dessus du foin, les nids secondaires ont été délaissés, et les progrès de la construction sont devenus très rapides dans le nid principal. Trois semaines après la substitution, l'aspect du nid est redevenu quasi normal, et l'on ne voit plus que quelques brins de paille sortir de sa base. Il est facile de les en extraire et de constater que les Fourmis ne les ont pas sectionnés, bien qu'elles le puissent très probablement.

Enfin, dans une autre expérience qui a porté sur une fourmilière de petite taille, mais très active, j'ai enlevé également tous les matériaux du nid et les ai remplacés par des feuilles mortes. Dès l'apparition des brindilles au-dessus des feuilles, je remettais une autre couche de feuilles mortes. L'expérience s'est arrêtée au début de l'automne, moment où l'activité constructrice est réduite ou nulle ; mais le nid avait alors atteint le double du volume initial, et les Fourmis n'en paraissaient pas incommodées.

On peut donc conclure que les Fourmis rousses s'accommodent très facilement de matériaux très variés, mais qu'elles n'utilisent que les brindilles qui peuvent seules se transporter.

### *La régulation de la construction à la surface du dôme.*

Comme je le disais au début, la forme régulière du dôme des Fourmis ne frappe pas tout d'abord. On a tendance à la considérer comme tout à fait naturelle, parce qu'on a dans l'esprit l'image d'un homme vidant d'une assez grande hauteur un panier de brindilles ; et, dans ce cas, elles se disposent en effet en tas régulier. Mais ce n'est point ainsi que procèdent les Fourmis : il faut songer qu'elles apportent leurs brindilles une par une, en les hissant assez péniblement sur les flancs de la fourmilière ; elles paraissent les y déposer *au hasard* (tout au moins pour un observateur hâtif, car certains faits me donnent à penser qu'il n'en est rien). Dans

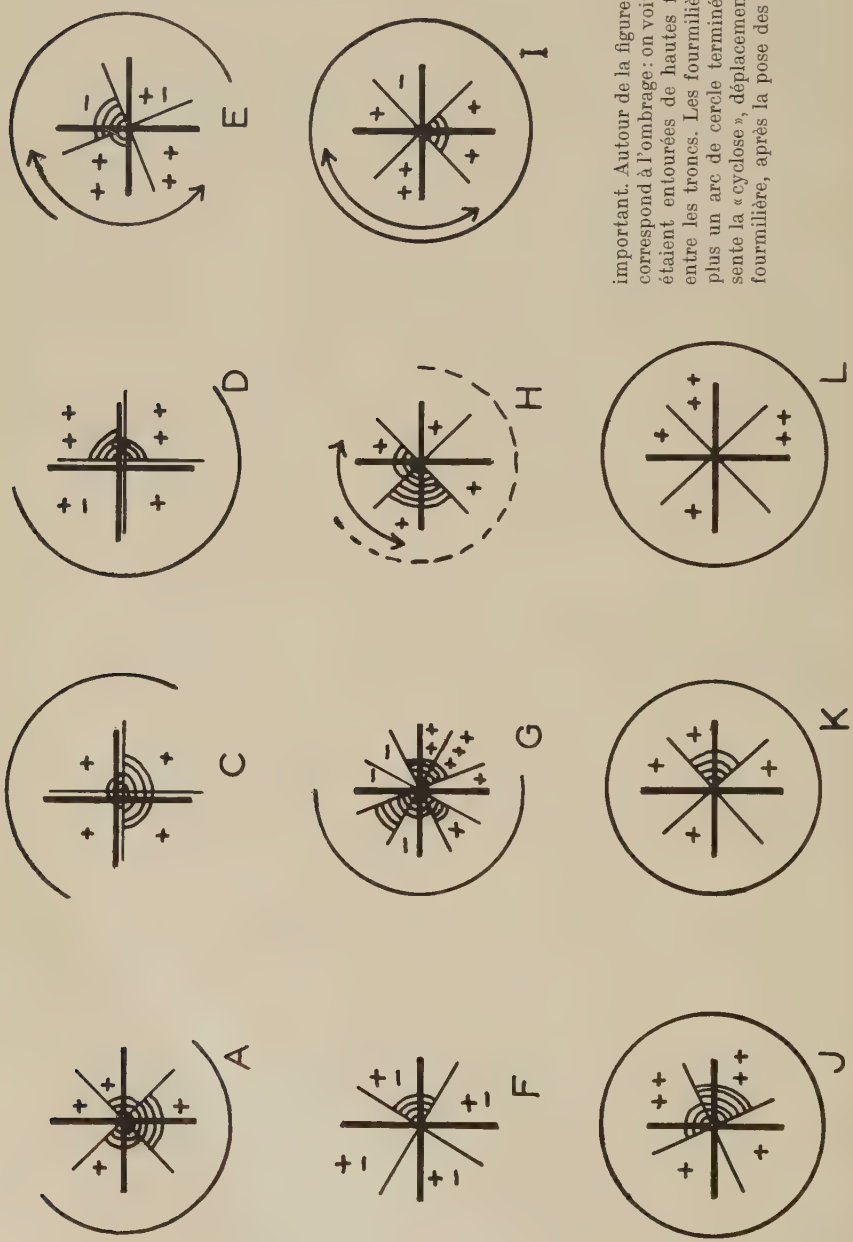


Fig. 2. — Cette figure résume les expériences sur la construction et le rôle des cloisons. La croix en traits épais correspond aux points cardinaux, la croix en traits minces à la direction des cloisons. Les petites croix, qui se trouvent entre les branches de la grande, rendent compte des différences d'activité locomotrice. Les secteurs circulaires parallèles qui rejoignent parfois les branches de la croix correspondent à l'activité constructive : on en a tracé d'autant plus que l'amas de brindilles entre les deux cloisons considérées a été plus important. Autour de la figure on voit que plusieurs fourmières étaient entourées de hautes futaies sans aucun hiatus entre les troncs. Les fourmières E et I comportent en plus un arc de cercle terminé par des flèches : il représente la « cyclose », déplacement rapide tout autour de la fourmière, après la pose des cloisons.



ces conditions, il n'y a pas de raisons pour que le dôme n'affecte point une forme tout à fait irrégulière, ce qui lui arrive d'ailleurs lorsque des obstacles gênent la construction. Or, dans la plupart des cas, ses contours sont, au contraire, régulièrement arrondis.

Il m'a semblé qu'il devait être possible de troubler la régulation — si elle existe —, en interposant des cloisons, comme l'a fait mon collaborateur DARCHEN sur les Abeilles. J'ai donc commencé par placer au sommet du dôme un croisillon de bois, de verre ou d'ardoise, dont les dimensions approximatives sont données dans la figure. Il n'était enfoncé au milieu des brindilles que de 2 ou 3 cm, ce qui est suffisant pour l'affermir ; par conséquent, la communication n'était pas coupée dans la zone profonde.

Ce cloisonnement a provoqué des perturbations considérables. D'abord, dans l'activité générale : dès le lendemain, lorsque l'agitation causée par l'intervention expérimentale est calmée, on note que, dans la très grande majorité des fourmilières, les Fourmis sont fort actives dans un ou deux des secteurs, alors que les autres sont à peu près déserts. C'est tout juste si l'on aperçoit dans les secteurs inactifs quelques ouvrières près des orifices de la fourmilière. Dans 50 % des cas apparaît un autre phénomène très curieux, et dont j'ignore la signification : c'est une circulation active dans les deux sens, une « cyclose » à la périphérie de la fourmilière ; circulation qu'on ne voit pas dans les nids intacts, où les déplacements, d'ailleurs assez peu actifs, paraissent uniformément répartis.

Enfin, au bout de quatre à six jours, suivant les conditions météorologiques, apparaissent des *dissymétries dans la construction*. Un ou deux secteurs (rarement trois) se développent plus que les autres, et le tas de brindilles monte alors très vite le long des croisillons ; les autres secteurs, moins actifs, ne tardent pas à présenter une dénivellation de 4 à 5 cm. Si la hauteur des croisillons ne dépasse pas 10 cm, l'amoncellement des brindilles atteint bientôt le bord supérieur de la paroi. Alors la construction se régularise et le dôme, où le croisillon se trouve désormais noyé, reprend sa forme primitive. La pose de cloisons supplémentaires, qui forment une étoile à huit branches, et non plus une croix, paraît rendre le phénomène plus net encore.

*Si, au lieu de cloisons, on utilise des plaques perforées, le dôme garde sa régularité.* Les meilleurs résultats sont obtenus avec des plaques de tôle perforées de trous de 4 mm de diamètre, espacés de 2 mm. On voit fort bien alors les Fourmis les traverser et même passer des brindilles à travers les trous. Mais, pour conserver la régularité du dôme, il ne suffit pas de quelques orifices, il en faut, semble-t-il, un grand nombre. Si, dans un croisillon de bois plein, on pratique de longues et larges fentes auprès du point d'intersection, là où les différences de construction sont les plus apparentes (fentes verticales de 5 cm de long sur 1 cm de large), les irrégularités n'en apparaissent pas moins.

On peut donner à l'obstacle une tout autre forme, par exemple, celle d'une enceinte circulaire de carton, ou de métal, posée au sommet du

dôme : par exemple, une boîte de métal de  $20 \times 8$  cm placée, l'ouverture en haut, au sommet de la fourmilière. Les Fourmis ne l'explorent que dans le premier moment, puis la désertent très vite. Peu à peu l'amoncellement des brindilles atteint le bord supérieur de la boîte, puis le dépasse. Ce n'est que très tardivement (au bout de cinq à huit jours) que quelques brindilles apparaissent au fond de la boîte. Il faut parfois quinze jours pour qu'elle soit à moitié pleine.

On peut supposer que le contact du métal éloigne les Fourmis et utiliser alors un cylindre de carton de 30 cm de diamètre et d'une hauteur variant entre 6 et 18 cm. La perturbation est assez forte ; même si la hauteur ne dépasse pas 6 cm, seules les fourmilières les plus actives (il existe d'énormes différences à ce point de vue) arrivent à combler le cylindre le plus bas en cinq à six jours. Certaines le laissent vide quasi indéfiniment. Quant au grand cylindre (parois de 18 cm), je n'ai trouvé qu'une fourmilière sur douze capable de l'emplir : elle se trouvait en phase de reconstruction très active (après une substitution de matériau) et ne mit guère plus de six jours à combler le cylindre de 3 à 4 litres de brindilles.

## DISCUSSION

L'interprétation de ces résultats se trouve gênée par diverses circonstances. En particulier, je n'ai pu encore découvrir de méthode pratique pour mesurer l'activité constructrice. J'avais bien planté en diverses zones des baguettes porteuses d'encoches équidistantes et numérotées et tenté d'évaluer la montée des brindilles le long des baguettes. Mais, au bout de peu de temps, les repères se trouvent inclinés par le processus continu de construction ; il vaudrait mieux employer de longues tiges métalliques, dont je ne disposais pas à ce moment. Il m'est donc impossible pour l'instant de donner des mesures quantitatives. Notons, toutefois, que l'activité de construction est diffuse, assez lente, se poursuivant même sous la pluie (colonies puissantes) et n'a rien de commun avec l'agitation que l'on peut observer en particulier après une longue période de mauvais temps.

J'ai essayé aussi de relier à un facteur externe les dissymétries de la construction suivant les secteurs, mais je n'ai pu aboutir jusqu'à présent. Ni la direction par rapport aux points cardinaux, ni celle des rayons solaires à certains moments de la journée (surtout le matin, moment de grande activité des Fourmis) ne m'ont fourni de corrélations valables. L'accroissement différentiel se produit aussi bien à l'ombre qu'au soleil, ou dans une clairière de 1 à 2 m de diamètre, entourée de haute futaie de toutes parts, et qui ne reçoit que le soleil de midi ; elle se produit aussi facilement par temps couvert que par beau temps ; avec des cloisons de verre ou des cloisons opaques. Les différences de microclimat entre les secteurs, induites par les cloisons, ne peuvent pas, à mon sens, rendre compte des troubles dans la régulation de la forme.

Il est préférable sans doute de rattacher les différences à une dissymétrie *endogène*. Ce ne peut être la présence du couvain ni celle des reines, puisque les déplacements de l'un et des autres sont nombreux et fréquents. On pourrait alors se référer aux travaux de CHEN et COMBES, qui mettent en évidence une grande différence entre différentes fonctions physiologiques et notamment entre l'activité constructrice, chez les ouvrières. Certaines Fourmis iraient en chercher d'autres et les porteraient dans la zone où le travail doit s'effectuer. On peut supposer que ces ouvrières actives sont en assez petit nombre et circulent à la surface du dôme suivant des voies plus ou moins circulaires et concentriques ; alors les cloisons radiales gêneraient beaucoup cette circulation et provoqueraient la fixation en une zone limitée du dôme, où les brindilles s'amasseraient plus vite qu'ailleurs. Dans le cas des cloisons perforées au contraire, le passage d'un secteur à l'autre est continu, comme l'observation la plus simple permet de s'en rendre compte ; et, corrélativement, les ouvrières peuvent conserver au dôme sa régularité.

Ce n'est qu'une hypothèse de travail, et fort incomplète. Elle n'explique pas, en effet, pourquoi les ouvrières ne contournent pas l'obstacle (qu'elles peuvent aussi parfaitement escalader, bien qu'elles ne le fassent que rarement). Rien ne les empêche *apparemment* de se répartir également dans tous les secteurs ; et pourtant (du point de vue de l'activité pure, non en relation fixe avec l'activité de construction) un quadrant très agité peut ne se trouver séparé d'un autre aussi désert que par une mince cloison ; et ils ne montrent guère de tendance à s'égaler. Enfin, des expériences (encore trop peu nombreuses) m'ont prouvé que la répartition des secteurs actifs par rapport aux inactifs peut se trouver modifiée par un simple enlèvement des cloisons, suivi de leur remplacement un quart d'heure après dans la même position. Si ce fait est vérifié ultérieurement, il sera en faveur de l'existence d'ouvrières « actives » qui se bloquent au hasard dans un des secteurs.

On peut rapprocher aussi ces expériences de celles de DARCHEN sur l'Abeille. Lorsque cet auteur interpose des cloisons métalliques sur la crête d'un rayon en construction, alors les Abeilles ne construisent plus de ce côté, mais seulement du côté opposé. Si bien qu'il se développe une forte dissymétrie. Par contre, lorsqu'il pratique une série d'orifices sur la plaque, la construction recommence et englobe peu à peu toute la plaque métallique. Là aussi, les Abeilles pourraient contourner l'obstacle ; mais ne le font que dans certaines conditions.

D'où il faut conclure que, chez les Abeilles et les Fourmis, les régulations de construction exigent qu'il n'y ait pas d'obstacle à la surface du nid.



## BIBLIOGRAPHIE.

1937. CHEN (S. G.). — The leaders and followers among the ants in nest building (*Physiol. Zool.*, **10**, 437-455).
1956. DARCHEN (R.). — Régulations de la construction sociale chez *Apis mellifica* (*Thèse*, Paris, en cours de publication).
1956. KLOFT (W.). — Zur Nestbautätigkeit der Roten Waldameise (*III<sup>e</sup> Congrès Un. Internat. Ét. Ins. Soc.*, Paris, Comptes rendus).
1929. STEINER (A.). — Temperaturuntersuchungen in Ameisennestern mit Erdkuppeln, im Nest von *Formica exsecta* und im Nestern unter Steinen (*Z. vergl. Physiol.* **9**, 1-66).

*Summary.*

One can replace the needles which constitute normally the building material of an ant hill's dome by pine cones or even by bits of hay, etc. The ants quickly cover these things with needles, and the hill resumes its former appearance. Any foreign object placed on the unbroken dome of the hill is either covered with needles or carried away. This is why the dome always look so orderly and free of things which do not belong there.

Little wooden rods of the size of a match stuck vertically into the dome can be removed by ants; but, several times, sticks of the length of a pencil and of a thickness of 3-4 mm, stuck in at right angles were first laid down horizontally and then covered up. Threads of little bits of rope were just covered.

If one lays out match sized sticks forming regular circular patterns, the disturbance is quickly eliminated, irrespective of where it was. If little wooden boards, about 20 cm high are stuck into the dome to a depth of 3-4 cm, considerable difference appear almost at once in the ants activity: in one quadrant, or, at the utmost, in two of them, they will work; and nearly completely neglect the other two. This is not so if the boards are perforated and allow the ants to pass through them. Evidently, the regularity of the building of the dome presupposes a net of communications beneath. Compare with DARCHEN's work on bees.

If a funnel made of boards is placed on the top of the dome, it is full of needles in a week or two, but only if it is not too high.

---

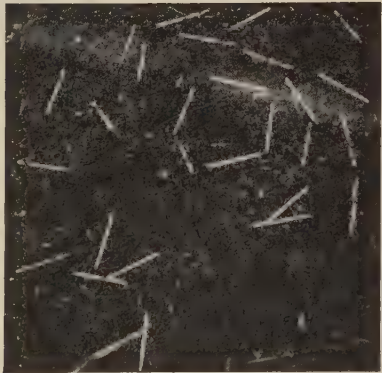
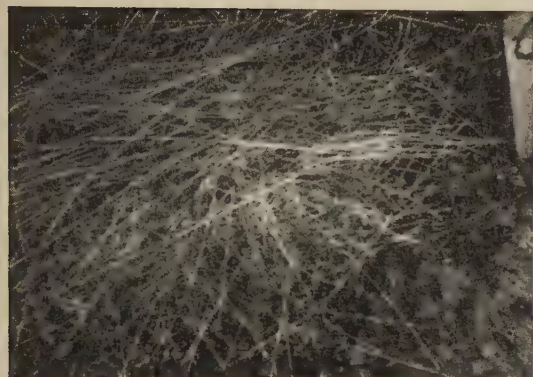


PLANCHE I. — 1 et 2 : remplacement des brindilles de la fourmilière par du foin ; en 2, les brindilles apparaissent deux semaines après et recouvrent progressivement le foin. — 3 : remplacement des brindilles par de la fibre de bois (blanche) : des brindilles plus sombres apparaissent très rapidement entre les fibres. — 4, 5, 6 : trois phases de la dislocation de couronnes d'allumettes posées sur la fourmilière (5, une heure après ; 6, à la fin de la journée).



7



8



PLANCHE II. — 7 et 8 : une couronne d'allumettes plantée sur la fourmilière est enlevée deux heures après par les fourmis ; en même temps, des feuilles de papier, trop grandes pour être transportées, sont recouvertes de brindilles.



9

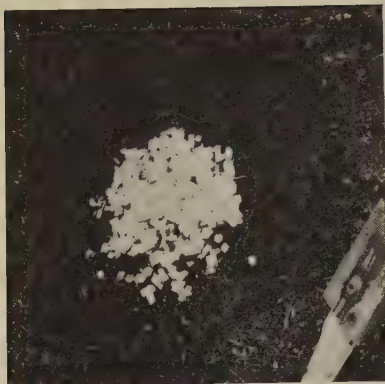


10



PLANCHE III. — 9 et 10 : de longues baguettes de la taille d'un crayon sont couchées au bout de huit jours.

11



12



16



PLANCHE IV. — 11 et 12 : de petits fragments de papier de la taille de confetti sont en grande partie transportés au bout de 4 à 5 heures. — 13 : discordance dans la construction de part et d'autre d'une cloison métallique ; on la voit aussi en 14, où les cloisons sont de verre ; par transparence, on aperçoit, en noir derrière la cloison de gauche, un amas de brindilles plus haut que sur le devant de la figure. — 15 : énormes différences d'activité locomotrice de part et d'autre d'une cloison de verre ; à gauche, le pointillé noir correspond à des fourmis, et contraste avec la partie droite de la figure, où le dôme est quasi désert ; seules quelques fourmis sont restées auprès des entrées. — 16 : un grand cylindre de carton, posé sur la fourmilière, est rempli au bout d'une dizaine de jours.



# THE RELATION OF STRIDULATION BEHAVIOUR TO ECOLOGY IN CERTAIN GRASSHOPPERS

by P. T. HASKELL

(Anti-Locust Research Centre, London.)

## INTRODUCTION

The most important published work relating to the ecology of British grasshoppers (DIVER & DIVER, 1933; CLARK, E. J., 1948; RICHARDS & WALOFF, 1954) has been concerned with the size and density of populations and the distribution of these in given habitats. The factor of movements of individuals and of groups of insects or even groups of species, implicit though it has been in the ecological results discussed, has hardly ever been the subject of experiment or even of hypothesis. CLARK (1948), it is true, carried out preliminary experiments on the movements of adults of *C. parallelus* and *brunneus*, while RICHARDS & WALOFF (1954) made a more detailed study of small scale movements in four species by statistical analysis of population densities and of data provided by the capture, marking, release and re-capture of insects. However, no detailed behavioural or physiological experiments have been made hitherto into the interesting phenomenon evinced by these grasshoppers of movements in relation to longterm changes of vegetation and what may be called "colony coherence"—that is, the ability of a colony of these insects to maintain its existence over periods of several years despite the existence of factors tending to disperse it, such as seasonal and long-term vegetation changes and individual movement. The present author, during a study of the stridulation behaviour of four species of grasshopper, was led to the conclusion that this behaviour played an important role in the ecology of the species in relation to these problems of movement and coherence, and the present paper presents a hypothesis concerned with this inter-action.

## DATA

The biology and population dynamics of several species of grasshopper occurring at the Imperial College Field Station in Berkshire, England, has been worked out by RICHARDS & WALOFF (1954). Of the species investigated ecologically four have been examined physiologically and ethologically from the point of view of stridulation and associated behaviour by the present author (HASKELL, 1955 a, b, 1956 a, b, 1957 a, 1958). These species were *Stenobothrus lineatus* (Panz), *Omocestus viridulus* (Linn), *Chorthippus parallelus* (Zett) and *Chorthippus brunneus* (Thunb).

The males of these grasshoppers all stridulate and have a repertoire of songs used in relation to different phases of behaviour (FABER, 1932). The present author has investigated in some detail the behaviour associated with the "normal" and "courtship" songs of the species (HASKELL, 1957 a, 1958). With normal males in the laboratory singing groups are formed consisting of two or more insects; there is little or no locomotor activity within these groups which are themselves static. If however a male is isolated for 24 hours or more, then returned to an observation cage containing a group of singing males, it will make its way towards them and join them. It may



only join the group acoustically, that is, it makes its way towards them presumably until the intensity of group song is perceived at some pre-determined level and then remains stationary, but now joining in the group singing.

Males of these species once mature will always sing the courtship song and attempt to mate with a female of the same species whenever she comes within visual range. Successful copulation, which means the transfer of a spermatophore, only interrupts the normal pattern of courtship behaviour in a male for a period of a few hours, after which he is again ready for mating.

The behaviour of females in response to male song is more complicated (HASKELL, 1958). From the time of the final moult to that of sexual maturity, females take no notice of male song of any type. When mature, the female becomes responsive to male song and shows a typical pattern of behaviour. This is similar in all the four species, and the response to normal song consists of three phases: response stridulation, orientation towards and locomotion to the male. Arrived near the male, the female stridulates in response to male song; in the case of *C. parallelus*, where the females are brachypterous, the insects make stridulation response movements with their hind legs which are similar to those made by the male during the production of normal song, but no audible sound is produced. The male, on noticing the female, sings the courtship song, and copulation generally ensues.

After complete copulation, the female becomes unresponsive to male song; if the female is isolated from males after mating, she recovers the responsive state in a period of from 6-20 days dependent on the species. This recovery is delayed or prevented if the females are kept after copulation with males or within sound of their normal song; in many cases the females die without recovering the responsive state. In responsive females, the response is also inhibited for periods of up to 24 hours prior to oviposition and is regained shortly afterwards; it is lost some days prior to death.

In these Acrididae, the normal song of the males seems to be completely intra-specific, and no responses have been noted in any species to songs other than their own.

## DISCUSSION

From the beginning of research on the problems of stridulation and associated behaviour in Orthoptera, many theories have been advanced to explain the phenomena and relate them to other facets of life in these insects. It is probably true to say that at the present time the theory that has most favourable currency is that which characterises insect stridulation as serving purposes exclusively related to reproduction in the various species known to sing. This idea has been for the most part based on the work of REGEN (1923, 1930) and FABER (1932) and embodies the view that in the Orthoptera the main use of stridulation lies in bringing the sexes together for mating. This view is supported also in the Homoptera by the work of OSSIANNILSSON (1949) and more recently in the Heteroptera by the observations of LESTON (1957) and HASKELL (1957 b). It was perhaps best expressed by POULTON (1896) "that . . . in sound producing species the power seemed almost without exception to be exercised with direct reference to the females". HOWEVER, the work of JACOBS (1950), WEIH (1951), BUSNEL & LOHER (1953) and HASKELL (1957 a) has shown the existence of complicated song behaviour between males which does not appear to be related to reproduction. We therefore must invoke a further general theory to attempt to explain it. This

theory, suggested by MYERS (1929) in relation to the singing of Cicadas and by LUTZ (1924) for Orthoptera, proposes that stridulation keeps a "colony" of insects together and serves to help them move to new habitats or feeding areas as a group. I hope to show that both these theories apply in an inter-dependent manner to the stridulation behaviour of the four species studied and that the overall picture so obtained clearly relates this behaviour to the ecology of these species. It must be emphasised that the hypothesis advanced here is only intended to apply to Acrididae with highly developed stridulation behaviour of a type similar to that described above. In certain Acrididae (e.g. *Locusta migratoria*) stridulation behaviour apparently plays only a minor role in relation to copulation, and clearly in these and in the silent species the present hypothesis will not hold.

To begin with, the structure of the so-called "colony" of grasshoppers as occurring at the place of observation must be defined. This is a term used by RICHARDS & WALOFF (1954) to define restricted areas of ground wherein the grasshopper density was much higher than in the intervening areas and which appeared to be persistent breeding sites. This localisation of the occurrence of grasshoppers has been noted and commented on by many observers, notably GRASSÉ (1929), RANDON (1932), CLARK (1948) and CHAPMAN (1952). The conclusions of the last two authors support the observations of RICHARDS & WALOFF that although there exists a "main colony centre" for the insects, movement out of and into this area takes place.

It must be remembered that in Britain these four species are at the northern extreme of their geographical distribution and the absolute numbers of any populations would be considerably less than in other parts of this range. Because of the corresponding relatively low population densities food supply never becomes either a matter for specific competition nor a limiting or initiating factor in movement. In work relating to the present day grasshopper fauna of Siberia, which includes the present four species, RUBTZOV (1932, 1935) describes general behaviour patterns which recall those of the present species. This is particularly so in relation to the exodus of young nymphs from the hatching areas, frequently in downhill movements as described by RICHARDS & WALOFF, and later in the return of mature females to higher ground for purposes of oviposition. RICHARDS & WALOFF also mention movements of the whole colony corresponding to major changes in the vegetation cover of the habitat. To these must be added the so-called appetitive behaviour movements of mature males seeking mates (JACOBS, 1953). It is clear from this work and that of CLARK (1948) and CHAPMAN (1952) that natural movement in the present species is by walking, with jumping and flight resorted to only after severe disturbance. RICHARDS & WALOFF (1954) indicate that in the colony as a whole small scale movements over a period of several days are so small, of the order of 60-90 cm, that special methods would be needed to detect them, and CLARK (1948) showed

that in *C. brunneus* and *C. parallelus* approximately 70% of marked groups of males and females were in the same place 10 days after release and 95% were within 5 metres of the point of release at this time. Both CLARK (1948) and CHAPMAN (1952) refer to this maintenance of grouping as the result of hypothetical "social reactions".

We can now consider the behavioural observations relating to stridulation against this ecological background; we shall first examine the behaviour of males. The general occurrence of "group singing" does not appear to be connected with sexual activity since a recently mated male displays the same reactions as an unmated insect. Males kept isolated for some time reacted on release by moving towards and joining singing groups. In the field such reactions would assist in keeping the males together in one area; the groups of singing males would act as sonic beacons to guide back a male which had wandered away from the main body. It may be objected that such a mechanism would only work over short distances. By using the data for the sensitivity of tympanal organs (HASKELL, 1956 a) and that for the intensity of the stridulation under field conditions (HASKELL, 1955 b) for these insects, it is possible to calculate the approximate ranges over which a male can hear the stridulation of one of its own species, although it must be borne in mind that this range will vary greatly with topography and microclimate. The distances for the various species are as follows: *O. viridulus* 140 cm; *S. lineatus* 50 cm; *C. brunneus* 200 cm; and *C. parallelus* 80 cm. These distances can be compared with the average length which can be jumped by the various species on disturbance; the following data are quoted from RICHARDS & WALOFF (1954), the first figure relating to females, the second to males; *O. viridulus* 55.6, 70.2 cm; *S. lineatus* 57.3, 74.0 cm; *C. brunneus* 69.8, 65.3 cm; *C. parallelus* 51.8, 43.1 cm. It can thus be seen that only in the case of *S. lineatus* would a single jump take the insect beyond the acoustic range of a group of its fellows; in the other species two jumps, sometimes nearly three, would be needed and this would only happen when there was severe disturbance in the habitat. However, the dense grass of the typical habitats of these species has an important effect in that visual fields will be very small. Thus a male even after wandering only a short distance may well lose sight of its fellows and from observations in the field it can be suggested that this is often the case. While remaining within acoustic range, however, the insects will sing in concert or alternately as the case may be and will not move very far. But acoustic as distinct from visual isolation will eventually produce the locomotor response to stridulation and so evoke movements tending to keep the males together. Direct field observations of such aggregating movements have been made by several observers; for example, CLARK (1948) describes observations on field populations of the present species where male stridulation produced aggregations of insects, which persisted for several days. He also carried out experiments with artificially arranged aggregations of *S. lineatus*, *C. parallelus* and *C. brunneus* and found that the cohesion of



these groups was high, in that about three-quarters of the insects remained in or near the 1 sq. metre test area for several days. He observed particularly interesting cases where 8 out of 11 males seen in the test area on successive days showed "sociable behaviour on the same spot and with the same individual". Again, CHAPMAN (1952) states in a discussion on the ecology of British grasshoppers "directive movements were made by males towards other (stridulating) males. Such response to stridulation may have the effect of aggregating individuals (males at least, females also if they can actually respond thus to stridulation) in suitable habitats".

Another function of group singing may be to attract newly emerged adult males of the species, and may provide an opportunity for the latter to learn (perhaps by imprinting) the typical song of the species, although the evidence available at present (e.g. JACOBS, 1953) suggests that song patterns are innate.

Stridulation and the behaviour associated with it might increase the effects of the predation and parasitism suffered by grasshoppers. Comparatively high density groups of insects may be expected to suffer greater predation than a dispersed population, especially from birds and small mammals. This is certainly so in the case of hopper bands of swarming locusts, where the density of the insects and their lack of cryptic coloration makes them the preferred targets for many birds, and several observations of the destruction of hopper bands by birds have been reported (e.g. ELLIS & ASHALL, 1957).

In the present species two factors would seem to act together to mitigate the disadvantages of grouping; one is their cryptic coloration, the other their comparative immobility. This puts a premium on visual orientation by predators and favours acoustically oriented attacks, at least from those with hearing organs capable of detecting stridulatory noises, for example birds. MARLER (1955) points out, on the assumption that most Orthopteran songs have their main energy in the region 6-14 kc/s, that such frequencies may well be difficult for the typical bird predators (Laniidae, Tetraonidae) to locate and are well above the range of maximum sensitivity of most birds. However, as has been shown (HASKELL, 1957 a, 1958), in the present four species the peak output is generally between 3-5 kc/s and thus location by predatory birds may be considerably easier. It is interesting to note that singing by several individuals rather widely dispersed as observed in the present species would tend to confuse acoustic orientation and reduce this danger, because the frequencies concerned are too high for phase-difference location, too low for intensity difference, and thus location must be on a time-difference basis, a difficult process for all except the larger birds whose ears are sufficiently wide apart to make this method practicable, and made more difficult still by the multiplicity of signals from the communal singers.

Group singing may have the disadvantage, however, of tending to attract predators, especially birds, to the aggregation area, where visual

methods may then supplant acoustic orientation. Here the immobility of the grasshoppers helps to re-inforce their cryptic coloration, and it is interesting to note (HASKELL, 1954, unpublished observations) that singing males can often be made to stop stridulating by moving some object in their overhead visual field. On the other hand CLARK (1948) cites evidence to show that the sight of large birds, such as kestrels, often releases jumping in the grasshoppers, a reaction which nullifies the use of cryptic coloration to some extent, although resumption of immobility after a jump may be disconcerting to birds (CLARK, 1948).

Males while singing sit still; furthermore, males and females while copulating and the latter while ovipositing are debarred from utilizing one of their defence adaptations—jumping power. Thus predation by such creatures as wasps and robber flies, listed by RICHARDS & WALOFF (1954) as predators of the present four species, may be facilitated at such times. In this connection it would seem that the observed inhibition of the response to song in females after a successful copulation, which would reduce the number of copulations occurring in any given population, would be advantageous in reducing the dangerous “exposure time” correlated with mating. Nor does the reduction in the number of copulations have any adverse effect on the population since it appears that females of the present species can, after one fertilisation, continue to lay viable eggs for the rest of their lives. It is clear that the relationship of field behaviour to predation and parasitism is most complicated and requires both further observation and experimental work. The only experimental work on this problem is that of RICHARDS & WALOFF (1954), who in some preliminary experiments were unable to show any effect of predation by birds on the grasshopper populations at Imperial College Field Station.

The role played by stridulation and the behaviour associated with it is clearly of great importance in promoting meetings of the sexes for mating. Two corollaries of this process must be noted; first, that the probable nature of the mechanism acts as a bar to inter-specific mating and secondly it may tend to help survival of a species by increasing the chances of mating in thinly populated areas around the fringes of a “colony”. The first point is of great importance in the preservation of a species. In the genus *Chorthippus* viable hybrids can be obtained by crossing a number of species (PERDECK, A. C. in JACOBS, 1955; KLINGSTEDT 1939) and in such circumstances stridulation behaviour may act as an effective isolator. This was thought by FULTON (1933) to occur in two physiological races of the cricket *Nemobius fasciatus* in which the major discernible difference between the races lay in the different stridulation patterns.

The consequences of stridulation behaviour between the sexes in tending to increase the number of matings on the fringes of a colony have of course a direct bearing on the maintenance of the population. In view of the mainly static habits of the present insects, such meetings would presumably

be very few if dependent entirely on random encounter, since apparently no other mechanism for bringing the sexes together exists; the findings of DEMPSTER (1955) even suggest that the grasshoppers exhibit certain reactions which would tend to prevent meetings of the sexes.

It is clear from the accounts given above of the reactions of females of the four species to male song that this behaviour would also favour the appearance and maintenance of aggregations. Females, when mature, would be attracted towards the (already grouped) singing males, courtship and copulation ensuing. The now non-responsive females may either remain in the group or, if they wandered away, may ultimately regain the responsive state and then be re-attracted to singing males. This general theory applies in a rather interesting way to the problems of oviposition. RICHARDS & WALOFF (1954) concluded that the most important reason for small scale movements of females was the seeking of suitable oviposition sites; if these sites existed some way from the preferred habitat or feeding area the females moved to them for purposes of oviposition. Stridulation behaviour, as summarised above, makes it clear that because of the non-responsive state of virgin females about to oviposit, and of mated females, these journeys would not be interrupted, nor would deviations occur due to reactions to male song, and the act of oviposition, one of great importance for the survival of the species, could also continue uninterrupted. Several possibilities as to the movement of females exist; they may leave and then return to the colony area; another alternative is that after migration from the nymphal habitat or feeding area to an area suitable for oviposition females stay there for the remainder of their lives. This latter possibility is supported by the evidence of RICHARDS & WALOFF (1954) who in experimental studies of small scale movements in the present four species came to the general conclusion that the nymphal stages of *C. brunneus* and *parallelus* moved downhill out of the oviposition hatching area, while mature females showed an uphill return movement probably in relation to the presence of oviposition sites. As mentioned before, RUBTZOV (1935) makes the same generalisation about the movements of grasshoppers in Siberia. DEMPSTER (1955) investigated the effect of vegetation on movement in these two species and concluded that nymphs and adult males tend to move from short to long vegetation, while adult females moved from long to short. It is interesting to relate these findings to observations on stridulation behaviour. Although it is known that some 3rd and 4th instar nymphs of the present species can stridulate (WEIH, 1951; JACOBS, 1953), the song patterns are irregular and the intensity very low (HASKELL, 1956, unpublished observations). Since it is unlikely that the tympanal organ becomes fully functional before the adult stage in these insects, it seems probable that the movement of nymphs is unaffected by acoustic behaviour. It may be postulated that the move into long grass is related to the larger temperature fluctuations and lower humidity and consequent danger of increased water loss in the short grass areas.



Nymphal populations entering the long grass habitat from the short would experience two changes; first, their rate of movement would be slowed down and extreme dispersal thus prevented and secondly they would tend to become visually isolated from other nymphs. On becoming adult, stridulation behaviour as previously described would tend to mitigate the disadvantages of this habitat from the point of view of courtship and mating behaviour. The movements of adult males into long grass may also be thought of as due to kinetic or taxic responses to physical features of the environment; the stridulation behaviour of adult males would in the new habitat tend to maintain the aggregations due to the environment.

However DEMPSTER'S (1955) findings that adult females tend to move out of the type of habitat favoured by males would clearly reduce the chances of meeting and copulation but stridulation behaviour would tend to counteract this effect at least until the females had copulated.

Females about to oviposit (in all the present species except *O. viridulus* which lays its eggs on and amongst the stems of grasses) would need to move away from this "feeding and mating" habitat and return to the "oviposition and hatching" habitat. The non-responsive state of mature mated females would release them from a behaviour pattern which might otherwise tend to attach them to the "feeding and mating" habitat.

Such an arrangement of dual loci for a colony can be compared with the hypothesis of KEY (1945) as regards the outbreak centres of *Chortoicetes terminifera*, the Australian plague grasshopper; he postulates the existence of "oviposition nuclei" and "food-shelter nuclei", portions of the habitat range which lie adjacent to one another and are "resistant to the loss of their characteristic features under extreme conditions." It is important to realise both in the case of *Chortoicetes* and the four species of British grasshopper that the "colony" is only a focus of a much more widely scattered population. It is the basis for a persistent population and thus must afford perennial properties of food and shelter for the main reproductive reservoir of the insect population. Should this focus shift, through physiographic or vegetation changes, the insect loci must shift with it. The occurrence of this duality of ecological requirement throughout the Acrididae has been stressed by URÁVÓV (1957).

Thus the apparent ability of the "colony" to move as a whole in relation to major changes in vegetation is of great importance. Similar movements are implicit in the observations of DIVER & DIVER (1933) and HARVEY (1938) on British grasshoppers. It may be postulated that physiographic and seasonal vegetation changes induce alteration of the habitat microclimate which results in kinetic or taxic movements of individual grasshoppers away from the changing area. What is more difficult to understand is why this process does not finally result in a spreading out of a colony and its eventual disappearance as a centre of relatively high-density population. It is clear that the behaviour associated with stridulation could play a part in mitigating this dispersion

effect during long-term movements by constantly "assembling" the population during the process of movement. Both CLARK (1948) and CHAPMAN (1932) believed in this possibility, the former doubting whether stridulation had only sexual significance and speculating on its "sociable" aspects, the latter presenting evidence in *C. brunneus* of the movements of parties over distances of twenty yards in which coherence was maintained presumably by stridulation.

It is interesting to speculate on this evidence as to whether in Acridids gregariousness is a distinguishing feature of their behaviour, appearing in a primitive form in these grasshoppers and reaching its highest development in the hopper bands and swarms of the locusts. The mechanisms are, of course, very different, but the essential feature of reaction to some quality of a fellow Acridid rather than to some feature of the environment is present in both cases. This is not to say that specific reactions to features of the environment are not present in both swarming and non-swarming species, but the development of gregariousness tends to overcome reactions to environmental features.

We thus see how two theories relating to stridulation, one of which postulates it as being subservient to sexual needs and the other as serving to keep the colony together, become interdependent when viewed against the background of the ecology of the insects. The colony needs to be kept together to increase the chances of mating in habitats that would otherwise render this difficult; the behaviour concerned in bringing the sexes together overcomes the dispersion of individuals in the habitat and at the same time reduces to a minimum the time spent by copulating pairs in the defenceless copulating position. Finally, the mechanism probably allows colonies to move in relation to major changes in environment without becoming dispersed. Once again it must be pointed out that this hypothesis is advanced only in respect of these species with highly developed stridulatory behaviour. The vast majority of Acrididae are silent, or apparently so, and in these cases the reasons for formation and maintenance of aggregations must be looked for elsewhere. The often repeated observations of localisation of both silent and singing species of grasshoppers in apparently uniform habitats (e.g. GRASSÉ, 1929; RANDON, 1932) have sometimes been explained by assuming a "gregarious instinct." This term, in the sense of KENNEDY (1951), presumes some form of inter-communication between individuals, and the present paper suggests that in some species at least the communication is acoustic.

### Summary.

1. The data available on the behaviour associated with stridulation in the following four species of Acrididae are summarized: *S. lineatus*, *O. viridulus*, *C. parallelus* and *C. brunneus*.

2. These data are discussed in relation to the ecology of the insects in

particular colonies in England, with reference to effects on mating, predation, oviposition and small and large scale movements in the field.

3. It is postulated that stridulation behaviour plays a dual role in relation to the ecology of the grasshoppers; it promotes meeting of the sexes and forms the basis of courtship and copulation behaviour and, secondly, it serves to maintain the grouping of a colony and to prevent dispersion of the latter during movement occurring in relation to changes in the vegetation of the habitat.

### *Sommaire.*

1. On étudie dans la présente note le comportement accompagnant la stridulation, chez les quatre espèces suivantes d'Acrididæ: *S. lineatus*, *O. viridulus*, *C. parallelus*, *C. brunneus*.

2. On discute ces comportements en fonction de l'écologie des Insectes observés dans des populations anglaises particulières; on s'attache plus spécialement à décrire la stridulation au cours de la période, du comportement alimentaire, de l'oviposition et des déplacements de plus ou moins grande amplitude dans la campagne.

3. On considère que la stridulation joue un rôle dans l'écologie des Criquets: elle amène la rencontre des deux sexes et constitue la base de la pariade et de l'accouplement, elle sert à maintenir la cohésion d'une colonie et prévient sa dispersion pendant les mouvements liés aux modifications de la végétation de l'habitat.

### *Zusammenfassung.*

1. In dieser Besprechung des Verhaltens von Heuschrecken im Zusammenhang mit der Stridulation werden folgende vier Arten angeführt: *S. lineatus*, *O. viridulus*, *C. parallelus* und *C. brunneus*.

2. Die Beobachtungen werden erörtert mit Bezug auf die Ökologie dieser Insekten in gewissen "Kolonieen", in England, mit Hinsicht auf Paarung, Räubertum, Eiablage, und großen und kleinen Bewegungen im Freiland.

3. Die Theorie wird aufgestellt daß das Stridulationsverhalten eine zweifache Rolle in der Ökologie der Heuschrecken spielt; i) es fördert das Auffinden zwischen Männchen und Weibchen und bildet die Grundlage für Balz und Kopulation; ii) es verhilft einer Kolonie ihre Gruppierung zu erhalten und verhütet ihre Zerstreuung wenn Bewegungen bezüglich Änderungen in der Vegetation des Fundortes stattfinden.



### Acknowledgements.

My thanks are due to Dr. B. P. Uvarov, Director, Anti-Locust Research Centre for reading and criticising the manuscript and to Miss A. H. BLANKLEY and Mrs. E. BLAXTER of the Anti-Locust Research Centre Library for assistance with references and in the preparation of the summaries.

### REFERENCES

1953. BUSNEL (R.-G.), LOHER (W.). — Recherches sur le comportement de divers Acridoidea mâles soumis à des stimuli acoustiques artificiels (*C. R. Acad. Sci., Paris*, **237**, 1557-1559).
1952. CHAPMAN (K.). — Ecological studies on solitary Acrididæ in England and South Africa (*J. ent. Soc. S. Afr.*, **15**, 165-203).
1948. CLARK (E. J.). — Studies in the ecology of British grasshoppers (*Trans. R. ent. Soc. Lond.*, **99**, 173-222).
1955. DEMPSTER (J. P.). — Factors influencing small-scale movements of some British grasshoppers [*Proc. R. ent. Soc. Lond.*, (A), **30**, 145-150].
1933. DIVER (C.), DIVER (P.). — Contributions towards a survey of the plants and animals of South Haven Peninsula, Studland Heath, Dorset. III. Orthoptera (*J. Anim. Ecol.*, **2**, 36-69).
1957. ELLIS (P. E.), ASHALL (C.). — Field studies on diurnal behaviour, movement and aggregation in the Desert Locust (*Schistocerca gregaria* Forskal) (*Anti-Locust Bull.*, No. **25**, 94 p.).
1932. FABER (A.). — Die Lautäusserungen der Orthopteren II. Untersuchungen über die biozönotischen, tierpsychologischen und vergleichend-physiologischen Probleme der Orthopterenstridulation. Methodik der Bearbeitung und Auswertung von Stridulations-beobachtungen (Einzeldarstellungen) (*Z. Morph. Okol. Tiere*, **26**, 1-93).
1933. FULTON (B. B.). — Inheritance of song in hybrids of two subspecies of *Nemobius fasciatus* (Orthoptera) (*Ann. ent. Soc. Amer.*, **26**, 368-376).
1929. GRASSÉ (P.-P.). — Étude écologique et biogéographique sur les Orthoptères français (*Bull. biol.*, **63**, 489-539).
1938. HARVEY (L. A.). — Preliminary note on the relations between grasshoppers and the recolonisation of denuded heath-and moor-land vegetation (*Trans. Soc. Brit. Ent.*, **5**, 291-297).
- 1955 *a*. HASKELL (P. T.). — Vibrations of the substrate and stridulation in a grasshopper (*Nature, Lond.*, **175**, 639-640). — 1955 *b*. Intensité sonore des stridulations de quelques Orthoptères britanniques [*In* BUSNEL (R.-G.), éd.]. Colloque sur l'Acoustique des Orthoptères [*Ann. Epiphyt.* (fasc. hors sér.), 154-167]. — 1956 *a*. Hearing in certain Orthoptera. I. Physiology of sound receptors (*J. exp. Biol.*, **33**, 756-766). — 1956 *b*. Hearing in certain Orthoptera. II. The nature of the response of certain receptors to natural and imitation stridulation (*J. exp. Biol.*, **33**, 767-776). — 1957 *a*. Stridulation and associated behaviour in certain Orthoptera. I. Analysis of the stridulation of and behaviour between males [*Brit. J. Anim. Behav.*, **5**, 139-148]. — 1957 *b*. Stridulation and its analysis in certain Geocorisæ (Hemiptera Heteroptera) [*Proc. zool. Soc. Lond.*, **129**, 351-358]. — 1958. Stridulation and associated behaviour in certain Orthoptera. II. Stridulation of females and their behaviour with males [*Anim. Behav.*, **6**, 27-42].
1950. JACOBS (W.). — Vergleichende Verhaltensstudien an Feldheuschrecken (*Z. Tierpsychol.*, **7**, 169-216). — 1953. Verhaltensbiologische Studien an Feldheuschrecken (*Z. Tierpsychol.*, Beiheft **1**, 1-228). — 1955. Problèmes relatifs à l'étude du

- comportement acoustique chez les Orthoptères [*In* BUSNEL (R.-G.), éd.]. — Colloque sur l'Acoustique des Orthoptères [*Ann. Epiphyt.* (fasc. hors sér.), 307-318].
1951. KENNEDY (J. S.). — The migration of the Desert Locust (*Schistocerca gregaria* Forsk.). I. The behaviour of swarms. II. A theory of long-range migrations [*Phil. Trans.*, (B), **235**, 163-290].
1945. KEY (K. H. L.). — The general ecological characteristics of the outbreak areas and outbreak years of the Australian Plague Locust (*Chortoicetes terminifera* Walk.) (*Bull. Coun. Sci. industr. Rest. Aust.*, no. **186**, 1-127).
1939. KLINGSTEDT (H.). — Taxonomic and cytological studies on grasshopper hybrids. I. Morphology and spermatogenesis of *Chorthippus bicolor* Charp. X *Ch. biguttulus* L. (*J. Genet.*, **37**, 389-420).
1957. LESTON (D.). — Sound production in Hemiptera Heteroptera. Stridulatory mechanisms in terrestrial species [*Proc. zool. Soc. Lond.* **128**, 369-386].
1924. LUTZ (F. E.). — Insect sounds (*Bull. Amer. Mus. nat. Hist.*, **50**, 333-372).
1955. MARLER (P.). — Characteristics of some animal calls (*Nature, Lond.*, **176**, 6-8).
1929. MYERS (J. G.). — Insect Singers (*A natural history of the cicadas*). London, George Routledge et Sons Ltd., 304 p.).
1949. OSSIANNILSSON (F.). — Insect drummers (*Opusc. Ent.*, Suppl., **10**, 1-145).
1896. POULTON (E. B.). — On the courtship of certain European Acrididæ (*Trans. ent. Soc. Lond.*, 233-252).
1932. RANDON (J.). — Les groupements d'Orthoptères du Bas-Languedoc (*Bull. biol.*, **66**, 1-44).
1923. REGEN (J.). — Über die Orientierung des Weibchens von *Liogryllus campestris* L. nach dem Stridulationsschall des Männchens [*S. B. Akad. Wiss. Wien* (1), **132**, 81-88]. — 1930. Über den Aufbau der Stridulationslaute der saltatoren Orthopteren [*S. B. Akad. Wiss. Wien* (1), **139**, 539-544].
1954. RICHARDS (O. W.), WALOFF (N.). — Studies on the biology and population dynamics of British grasshoppers (*Anti-Locust Bull.*, no. **17**, 182 p.).
1932. RUBTZOVA (I. A.). — The habits and conditions of grasshopper outbreaks in East Siberia (In Russian with English summary) [*Bull. Pl. Prot. Leningr.* (1) no. **3**, 33-130]. — 1935. Regularities in the development and behaviour of Siberian Acrididæ in connection with climatic factors (In Russian with German summary) (*Bull. Acad. Sci. U. R. S. S.*, no. **5**, 789-824).
1957. UVAROV (B. P.). — The aridity factor in the ecology of locusts and grasshoppers of the Old World (*In Arid Zone Research. VIII. Human and Animal Ecology*. Paris, UNESCO, 164-198).
1951. WEIH (A. S.). — Untersuchungen über das Wechselsingen (Anaphonie) und über das angeborene Lautschema einiger Feldheuschrecken (*Z. Tierpsychol.*, **8**, 1-41).

*Note added in proof.*

Since this paper was written, PERDECK (1957) has published an important paper on "The Isolating Value of Specific Song Patterns in Two Sibling Species of Grasshoppers (*Chorthippus brunneus* Thunb. & *C. biguttulus* L.)", *Behaviour* **12**: 1-75. In these two sympatric species stridulation not only plays a part in isolation but forms almost the only effective mechanism for it, and it is suggested that isolation produced in this way is a primary and not a secondary manifestation, originating early in the history of species.

## ÉTUDES SUR LES FORMICIDÆ

### IV. SUR LE VENIN DU DOLICHODÉRIDE *TAPINOMA NIGERRIMUM* NYL.

Par M. PAVAN et R. TRAVE

(Institut d'Anatomie Comparée de l'Université de Pavie.)

Les venins des Hyménoptères constituent l'un des domaines dans lesquels nous avons déjà conduit et nous conduisons encore des recherches, dans le but de connaître leur nature et les propriétés biologiques en relation avec leur composition chimique et la structure de leurs composants. C'est ainsi que nous pouvons citer différents travaux sur cette question, travaux effectués avec divers collaborateurs ; il s'agit, en particulier, de recherches sur l'iridomyrmécine (PAVAN, 1951, 1952, etc. ; FUSCO-TRAVE-VERCELLONE, 1955 ; PAVAN-RONCHETTI, 1955 ; PAVAN-BAGGINI, 1955 ; PAVAN-VALCURONE, 1955), sur la dendrolasine (PAVAN, 1956 ; QUILICO, PIOZZI, PAVAN, 1956) et, plus récemment, sur les composants du venin de *Tapinoma nigerrimum* Nyl. (TRAVE-PAVAN, 1956). Dans ce dernier travail, nous avons reporté surtout les résultats de la recherche chimique : nous pensons qu'il est maintenant utile de reprendre le sujet sous un point de vue plus naturalistique, tout d'abord en le plaçant dans l'ensemble de données que nous possédons au sujet des appareils producteurs de venin et des sécrétions vénéneuses des Hyménoptères en général et des Formicides en particulier.

### CONNAISSANCES PRINCIPALES SUR LE VENIN DES HYMÉNOPTÈRES

Le fait de posséder un venin est un facteur très important dans la vie et dans le comportement d'une partie des Hyménoptères. Les Hyménoptères ne sont pas tous munis d'un appareil producteur de venin qui soit efficace ; dans les groupes qui le possèdent, seul le sexe féminin (ouvrières et reines) en sont pourvues. Il existe des groupes d'Hyménoptères Térébrants et Aculés qui sont tous ou en partie munis d'un appareil à venin typique, localisé dans la partie postérieure de l'abdomen et constitué par : une glande acide et une glande alcaline qui produisent la sécrétion, et par un appareil capable d'injecter le venin dans d'autres animaux ou dans des végétaux ; d'autres groupes d'Aculés (par exemple les Formicides de la famille des *Formiciniæ*) bien que possédant l'appareil glandulaire sécréteur typique (« appareil à coussinet ») ne sont pas en mesure d'injecter le venin dans le corps de la victime, par manque d'un organe adapté ; ils utilisent alors leur venin, en le mettant en contact avec le corps de la victime par aspersion, même à des distances notables.

D'autres Hyménoptères Formicides (famille des *Dolichoderinæ*) sont dotés d'un double appareil à venin : l'appareil typique avec glande acide,



glande alcaline et appareil injecteur, et un autre plus simple comprenant les glandes dites « anales » et le réservoir correspondant.

Les sécrétions des glandes mandibulaires des *Formicidæ*, qui peuvent aussi servir en partie à la protection, forment, au contraire, une catégorie à part.

L'étude des venins des Hyménoptères a été effectuée jusqu'à présent sur très peu d'espèces. Les recherches se sont surtout portées sur les points suivantes que nous citons à titre simplificatif et non limitatif :

- 1° Venin protecteur des Abeilles et des Guêpes ;
- 2° Venin paralysant des Braconides ;
- 3° Venin des Formicides produits par des glandes de l'abdomen :
  - a) Par l'appareil à coussinet (producteur d'acide formique) ;
  - b) Par les « glandes anales » (non productrices d'acide formique) ;
- 4° Venins de Formicides produits par les glandes mandibulaires.

Nous reportons maintenant quelques exemples illustrant les quatre points cités ci-dessus :

I. — Le venin d'*Apis mellifera* L a été étudié, tant au point de vue chimique qu'au point de vue biologique, par de nombreux auteurs ; cependant nous ne connaissons encore parfaitement ni sa constitution chimique, ni ses propriétés biologiques. Rappelons, par exemple, que, dans le venin total on aurait trouvé des substances de nature polypeptidique indéfinie, toxiques pour les homéothermes, de la lécithinase A, de l'histamine, de l'entéramine, de la riboflavine (vitamine B<sub>2</sub>), un facteur diffuseur (ialuronidase), etc. Ce venin aurait des propriétés neurotoxiques, histaminolibératrices, antibactériennes, insecticides, etc. Un bref résumé des principales questions signalées ici se trouve dans Brangi-Pavan, 1954 b.

Le venin de guêpe a été moins étudié que le venin d'Abeille ; dans ce venin on trouve : de l'histamine, de l'antéramine, une substance myocontracturante du groupe des kinines (dans la *Vespa vulgaris* L.) selon JAKES et SCHACHTER, 1954, et SCHACHTER et THAIN, 1954, confirmé, pour le venin de *Polistes gallicus* L., par les recherches de ERSPAMER, (1955), PAVAN (1955 a). Comme le venin d'Abeille, il a des propriétés neurotoxiques, antibactériennes, insecticides.

II. — Le venin des Braconides a été surtout étudié sur *Habrobracon juglandis* (Ashm.) par HASE (1924) et BEARD (1952) ; il a un effet curarisant sur les larves des Insectes qui servent de proie pour l'élevage de la progéniture. Bien que ce problème ait intéressé les savants dès le siècle précédent, on ignore encore complètement la nature chimique des venins paralysants.

III. — A propos des venins produits par les glandes de l'abdomen des Formicides, nous devons distinguer : A) le groupe des *Formicinæ* ; B) le groupe des *Dolichoderinæ*.

A) Dans les *Formicinæ*, c'est l'acide formique qui constitue la partie

biologiquement active du venin. C'est surtout STUMPER qui a effectué les études les plus intéressantes sur le venin des *Formicinæ*, quant aux résultats qualitatifs et quantitatifs au sujet de la présence d'acide formique, lequel existe en quantité vraiment surprenante et présente une concentration élevée (par exemple, selon STUMPER, dans les ouvrières de la *Formica rufa* L., le venin représente jusqu'à 20 % du poids du corps, et sa concentration en acide formique peut rejoindre 70 %). Récemment O'ROURKE, 1950, a exposé quelques hypothèses sur le mécanisme de formation de l'acide dans l'organisme producteur.

Le venin à l'acide formique des *Formicinæ* a naturellement toutes les propriétés biologiques caractéristiques de cette substance et constitue une arme d'attaque et de défense efficace et bien connue tant contre les Insectes compétiteurs que contre les autres animaux.

B) Dans les *Dolichoderinæ*, on doit distinguer — comme nous l'avons déjà fait remarquer — deux appareils producteurs de venin :

1° Un appareil à venin typique, avec glande acide et glande alcaline, qui, du moins en ce qui concerne les *Dolichoderinæ* européens, à cause de leur très petite taille, ne revêt que peu d'importance, étant petit et faible, malgré sa conformation normale et son appareil sécréteur fonctionnel ; cet appareil a été décrit par PAVAN-RONCHETTI, 1955, pour l'*Iridomyrmex humilis* Mayr.

2° Un appareil à venin constitué par les glandes dites « anales » qui produisent un venin se recueillant dans un réservoir bifurqué, lequel débouche, par l'intermédiaire d'un conduit unique, à l'extrémité de l'abdomen, entre le IV<sup>e</sup> et le V<sup>e</sup> urotergite (PAVAN, 1950 ; PAVAN-RONCHETTI, 1955).

Rappelons que divers *Dolichoderinæ* sont connus pour leur odeur particulière que l'on observe surtout quand on écrase l'animal. Cette odeur à laquelle on donne traditionnellement le nom d'odeur de *Tapinoma* est particulière à la sécrétion des glandes anales.

Jusqu'en 1948, les connaissances au sujet du venin des glandes anales des *Dolichoderinæ* étaient rares, contradictoires et surtout superficielles. C'est ainsi que selon les auteurs, l'odeur de *Tapinoma* était définie de différentes façons : par exemple pour MELANDER et BRUES, 1906 (et par la suite pour de nombreux autres auteurs), la sécrétion du *Forelius fetidus* (BUCKLEY) et de beaucoup d'autres espèces de Dolichodérides aurait une odeur semblable à celle de la noix de coco rance (*rancid cocoanuts*) et serait composée d'un éther (*sic*). D'après PATTON, 1931, le *Tapinoma sessile* (SAY) des États-Unis émane une odeur d'ananas (pineapple). En 1873, MOGGRIDGE rapporte que le *Tapinoma erraticum* Latr. a une odeur désagréable, semblable à celle de l'huile rance, tandis qu'en 1953, STUMPER dit que l'odeur de cette même espèce est éthérée, agréable, apparentée à celle de la mélisse (citronnelle). D'après BERNARD, 1946 et 1950, les femelles des Dolichodérides européens, *Botryomyrmex decapitans* Santschi, *B. regicidus* *B. corsicus* Em. sp. *laticeps* Em. ont une odeur d'acétate d'amyle, tandis que le *Tapinoma nigerrimum* Nyl. et le *Tapinoma simrothi* Krausse

émanent une odeur de beurre rance, c'est-à-dire d'esters butyriques.

Stumper 1921 rapporte que *Tapinoma erraticum* "sent la méthylhepténone", ce qui suffit à Forel 1922 (T. II, pag. 50) pour affirmer que "d'après Stumper l'odeur de *Tapinoma* est due à cette substance".

À notre avis, la typique « odeur de *Tapinoma* », du moins celle de la sécrétion du *Tapinoma nigerrimum* Nyl., est une odeur agréable. La différence de valutation des odeurs observée entre les différents auteurs, dépend probablement en partie de facteurs subjectifs, mais elle peut également correspondre en partie à des différences de constitution des venins, ce qui a été démontré — comme nous le verrons plus loin — pour différentes espèces de Dolichodérides, récemment étudiés à fond.

Un autre chapitre des recherches sur les venins de Dolichodérides s'est ouvert dans les travaux de PAVAN et de NASCIMBENE (1948), qui ont démontré la présence, dans l'extrait brut total d'ouvrières d'*Iridomyrmex humilis* Mayr. (Fourmi argentine), Dolichodéride privé d'odeur typique, d'un principe antibactérien auquel ils donnèrent le nom d'*iridomyrmécine*, et qui, par la suite, toujours en 1948, fut obtenu à l'état pur cristallisé par PAVAN. Les études successives ont démontré que l'*iridomyrmécine* est un produit nouveau, appartenant aux lactones, dont la formule est  $C^{10}H^{16}O^2$  (PAVAN, 1950, 1951 a, 1951 b) et qu'elle constitue le principe insecticide du venin des glandes anales de l'*Iridomyrmex humilis* Mayr. Par la suite, les recherches s'orientèrent, d'une façon plus détaillée, sur les propriétés biologiques de la nouvelle substance (PAVAN, 1955 a, b, c ; PAVAN-RONCHETTI, 1955 ; ERSPAMER-PAVAN, 1955), tandis que les recherches chimiques de FUSCO, TRAVE et VERCELLONE (1955 a, 1955 b) conduisirent à la connaissance de la structure de la substance, comme il résulte de la formule (I).

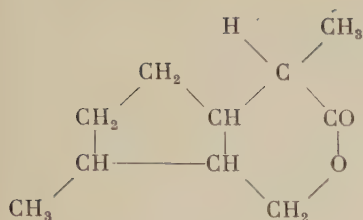
L'ensemble des études effectuées au sujet de l'*iridomyrmécine* constitue le cycle de recherches le plus complet et approfondi, tant au point de vue chimique que biologique et anatomique, effectué jusqu'à ce jour sur un venin d'Hyménoptères.

Entre temps, l'existence de facteurs antibactériens et insecticides a également été mise en évidence dans le venin brut de *Tapinoma nigerrimum* Nyl. et de *Liometopum microcephalum* Panz. (PAVAN-NASCIMBENE, 1948 ; PAVAN, 1949, 1952 b, c).

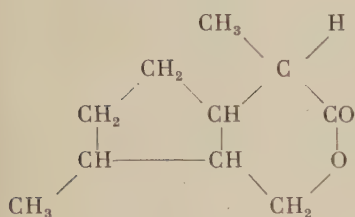
En 1953, CAVILL et FORD, en étudiant la composition chimique du venin d'*Iridomyrmex detectus* Sm. de l'Australie, obtinrent le méthylhepténone. Dans deux publications récentes, CAVILL FORD et LOCKSLEY (1956) ont fait savoir qu'ils ont extrait le méthylhepténone (V) et l'iridodial (III) de l'*Iridomyrmex conifer* (For.) et *I. detectus* (Sm.), l'isoiridomyrmécine (1) (II) du *I. nitidus* (Mayr.) et ont confirmé les recherches de PAVAN et de ses collaborateurs sur l'*iridomyrmécine* du *I. humilis* Mayr.

(1) Les auteurs australiens avaient d'abord donné à ce produit le nom d'iridolactone ; par la suite, ils ont reconnu que ce produit est identique à l'iso-iridomyrmécine. Cette substance avait déjà été décrite par PAVAN, 1951, 1952 (sur des données fournies par VERCELLONE) et par FUSCO, TRAVE, VERCELLONE, 1955 a, b.

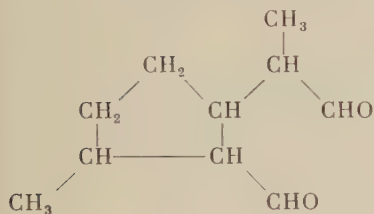




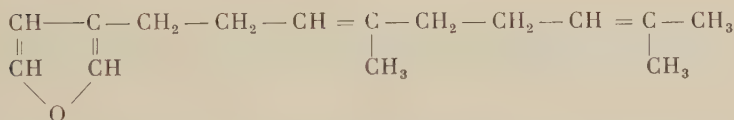
I. — Iridomyrmécine  $C_{10}H_{16}O_2$ ; lactone de l'acide  $\alpha$  [2-oxyméthyl-3-méthyl-cyclopentil] propionique.



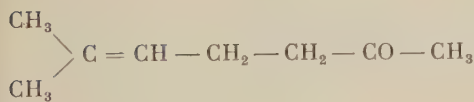
II. — Isoiridomyrmécine  $C_{10}H_{16}O_2$ .



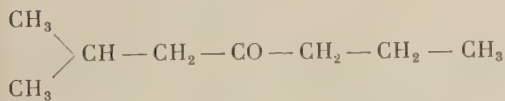
III. — Iridodial  $C_{10}H_{16}O_2$   
dialdéhyde de l'iridomyrmécine.



IV. — Dendrolasine  $C_{15}H_{22}O$   $\beta$ -(4,8-diméthyl-3,7-nonadiénil) furane.



V. — Méthylhepténone  $C_8H_{14}O$ .



VI. — Propyl-isobutyl-cétone  
 $C_8H_{16}O$ .

Entre temps nous avons effectué nos recherches sur le *Tapinoma nigerimum* Nyl., recherches qui nous ont permis d'obtenir des données nouvelles et d'autres données confirmant les observations des auteurs australiens ; nous avons reporté ces résultats, en particulier en ce qui concerne la chimie, dans Trave-Pavan, 1956.

IV. — Dans différentes espèces de *Formicidæ* du genre *Lasius*, la sécrétion des glandes mandibulaires a une odeur agréable caractéristique. Les premières recherches approfondies à ce sujet ont été conduites par PAVAN, qui a extrait de la sécrétion du *Lasius (Dendrolasius) fuliginosus* Latr. l'élément parfumé auquel il a donné le nom de *dendrolasine* (PAVAN, 1956). Les recherches de QUILICO, PIOZZI et PAVAN (1956) ont démontré que la dendrolasine est un produit nouveau, inconnu dans la littérature chimique, répondant à la composition centésimale  $C_{15}H_{22}O$  et ayant la structure (IV).

La dendrolasine, étant émise par l'animal irrité expérimentalement ou naturellement dans la lutte contre les Formicides compétiteurs, a un rôle défensif (PAVAN, 1955). Il faut donc la considérer comme un venin protecteur de type différent du venin habituel de l'appareil abdominal, tant en raison de son origine qu'à cause de la façon dont il est utilisé.

#### RECHERCHES SUR LE VENIN DES GLANDES ANALES DU *TAPINOMA NIGERRIMUM* NYL.

Comme nous l'avons vu avant nos recherches, la chimie du venin de *Tapinoma nigerrimum* Nyl. n'avait pas été étudiée.

Reprenant les données déjà citées, publiées par PAVAN et NASCIBENE en 1948, nous avons examiné le comportement des ouvrières deladite espèce, au sein de la nature, dans leur lutte contre les autres fourmis ou contre d'autres insectes, et nous avons constaté qu'elles emploient activement le venin de leurs glandes anales, tant pour l'offensive que pour la défensive, agissant conformément à ce que l'on observe en général à propos de beaucoup de Dolichodérides (1).

Si l'on extrait le réservoir des glandes anales du corps de l'animal vivant et si on l'ouvre sous l'eau, on en voit sortir le venin brut sous forme de liquide dense. Le venin flotte sur l'eau, exhalant l'odeur typique que l'on perçoit quand on écrase certaines fourmis. Quand l'odeur a disparu, par

(1) A ce point nous devons cependant observer que le fait de pouvoir disposer d'un venin insecticide ou tout au moins repoussant n'immunise pas les ouvrières de *Tapinoma* contre les agressions de certains Hyménoptères prédateurs qui attaquent souvent de façon sélective et paralysent les ouvrières de Dolichodérides pour les emmagasiner dans les alvéoles pédotrophiques. GRANDI (1951, II : 1221-1222), rapportant les observations de différents auteurs (ÉMERY, 1893 ; FERTON, 1890-1896 ; BIGNELL, 1900 ; HICKS, 1933 ; GRANDI, 1928-1935 ; PATE, 1942-1944) signale que les *Crabro* F. du sous-genre *Tracheliodes* A. Mor. emmagasinent dans leurs nids souterrains des ouvrières de Formicides Dolichodérides du genre *Liometopum* Mayr. et *Tapinoma* Forst. Des deux espèces européennes, le *Tracheliodes quinquenotatus* Jur. va à la chasse du *Tapinoma erraticum* Latr. et du *nigerrimum* Nyl., le *Tracheliodes curvitaris* Herr. Schæff. du *Liometopum microcephalum* Panz.

évaporation rapide, il reste sur l'eau un voile de substance pâteuse insoluble et incolore. La présence de cette substance, qui représente un composant du venin, avait déjà été signalée par les auteurs précédents qui signalent souvent l'engluement des insectes compétiteurs obtenus par les Dolichodérides en aspergeant l'ennemi avec le venin de leurs glandes anales (FOREL, 1877, 1920).

Au cours de nos recherches, portant sur de grosses quantités de *Tapinoma nigerrimum* Nyl. (environ 15 kg d'ouvrières, en plusieurs lots) obtenues grâce à des systèmes de capture et de conservation spéciaux, nous avons extrait le venin brut à l'aide de l'éther éthylique, et en isolant ses principaux composants nous avons obtenu le méthylepténone (V) et le propyl-isobutyl-cétone (VI).

Ces deux produits, agréablement parfumés, confèrent au venin total de *Tapinoma nigerrimum* Nyl. la typique « odeur de *Tapinoma* ». Ils sont présents dans le venin total dans la proportion de 1 de méthylhepténone pour 1,5 de propyl-isobutyl-cétone.

Nous avons en outre isolé une troisième substance, le produit  $C_{10}H_{16}O_2$  dont nous avons pu mettre en évidence la structure de dialdéhyde de l'iridomyrmécine (III) (1).

Tandis que le méthylepténone et le propyl-isobutyl-cétone sont des produits connus, l'iridodial était au contraire un produit nouveau dans la littérature chimique. La structure de ce produit présente une analogie intéressante avec celle de l'iridomyrmécine (le produit insecticide actif du venin de *Iridomyrmex humilis* Mayr.) analogie existant également au sujet de la dérivation possible de ces deux produits de résidus isopréniques.

### SIGNIFICATION POSSIBLE DES COMPOSANTS DU VENIN DE *TAPINOMA NIGERRIMUM* NYL.

Si l'on dissèque l'animal vivant, enlevant les glandes anales et le réservoir correspondant, on constate que le corps de l'insecte n'exhale aucune odeur caractéristique, tandis que cette odeur est nettement perceptible quand on libère le contenu du réservoir à venin : le méthylhepténone et le propyl-isobutyl-cétone sont donc les facteurs responsables de l'odeur de cette espèce, et sont exclusivement présents dans la sécrétion des glandes anales.

L'iridodial, liquide et incolore, est la substance que l'on trouve en ouvrant le réservoir sous l'eau ; elle affleure et forme la pellicule insoluble déjà signalée.

(1) Nous avons déjà effectué ces recherches, obtenant les résultats décrits, quand (1956) nous reçûmes une communication personnelle de G. W. CAVILL, qui nous informait qu'il avait extrait de Dolichodérides de l'Australie un dialdéhyde de l'iridomyrmécine auquel il avait donné le nom d' *iridodial*. Nous avons donc attendu, pour publier nos résultats, les publications de CAVILL et coll., annoncées comme imminentes, afin de confronter le produit annoncé par CAVILL et le dialdéhyde de l'iridomyrmécine obtenu par nous ; nous avons confirmé la correspondance des résultats dans la note TRAVE-PAVAN 1956.



L'iridodial à l'état pur, exposée à l'air et à la lumière, se polymérise en assumant une consistance pâteuse et une couleur jaune.

Tant le méthylepténone que le propyl-isobutyl-cétone, utilisée soit par contact direct soit à l'état de vapeurs, ont des propriétés insecticides non transcurables : ils ont été expérimentés sur de nombreuses espèces d'insecte et nous exposerons les résultats obtenus dans une publication sur ce sujet de Pavan et Ronchetti. Ces deux produits ont également de très modestes propriétés antibactériques, mises en évidences au cours d'expériences sur l'agar-germes et conduites en relation avec nos études par VALCURONE et BAGGINI (1957).

Au cours de nos recherches nous avons constaté que l'iridodial n'a qu'une faible activité insecticide ; elle est au contraire douée d'une activité antibactérienne supérieure à celle des deux autres produits.

Comme nous l'avons déjà dit, il faut considérer le méthylhepténone et le propyl-isobutyl-cétone comme des facteurs biologiquement actifs, au point de vue insecticide, du venin de *Tapinoma nigerrimum* Nyl., tandis que l'iridodial est un moyen engluant qui maintient plus longtemps en contact avec la proie les deux principes insecticides volatils, solubles dans cette substance, et de ce fait assume un rôle de potentiateur du venin.

Nous devons remarquer en particulier que, tandis que le méthylhepténone est un produit déjà connu dans la littérature entomologique, en raison de sa présence dans le venin d'*Iridomyrmex detectus* et de *I. conifer* de l'Australie (ainsi que dans certaines espèces végétales), le propyl-isobutyl-cétone est une substance qui, bien que connue, n'avait pas encore été trouvée comme composant du venin d'Insectes, et jusqu'à maintenant l'iridodial n'a été trouvée que dans trois espèces de Dolichodérides, à savoir : *Iridomyrmex detectus* (Sm.), *I. conifer* (For.) et *Tapinoma nigerimum* Nyl.

Avec ces recherches, le chapitre concernant la chimie du venin de *Tapinoma nigerrimum* Nyl. se conclut donc sur la démonstration des principales substances qui entrent dans sa composition.

Cependant il nous reste encore à étudier le chapitre de la biochimie de ces substances. L'étude de ce problème ultérieur bénéficiera indubitablement de l'ensemble des données déjà recueillies sur l'iridomyrmécine et de celles qui ont été obtenues au cours des recherches sur les *Iridomyrmex* de l'Australie.

— Institut d'Anatomie Comparée de l'Université de Pavie.

— Inst. de Chimie industrielle de l'Université de Milan ; Chaire de Chimie industrielle organique.

— Centre des recherches sur les antibiotiques et les insecticides d'origine animale Soc. Montecatini.

## LITTÉRATURE

1946. BERNARD (F.). — Notes sur les Fourmis de France. II. Peuplement des Montagnes méridionales (*Ann. Soc. Ent. de France*, **115**, 1-36). — 1950. Notes biologiques sur les cinq fourmis les plus nuisibles dans la région méditerranéenne [*Rev. de Pathologie végétale et d'Entomologie agric. de France*, **29** (1-2), 26-42].
1952. BEARD (R. L.). — The toxicology of *Habrobracon* venom: a study of a natural insecticide (*The Connecticut Agric. Exper. Sta. New Haven Bull.*, **562**, 1-27).
1954. BRANGI (G. P.), PAVAN (M.). — Sulle proprietà antibatteriche del veleno di *Apis mellifica* L. (*Hym. Apidae*) [*Insectes sociaux*, **1** (3), 210-217]. — 1954. Sulle proprietà antibatteriche del miele, propoli, pappa reale e veleno di *Apis mellifera* L. (*Hym. Apidae*) (*Mem. Soc. Ent. It.*, **33**, 19-32).
1953. CAVILL (G. W. K.), FORD (D. L.). — The chemistry of Ants (*Chemistry and Industry*, 351).
1956. CAVILL (G. W. K.), FORD (D. L.), LOCKSLEY (H. D.). — The chemistry of Ants [*Australian J. of Chem.*, **9** (2), 288-293]. — 1956. Iridodial and iridolactone (*Chem. and Industry*, 465).
1954. ERSPAMER (V.). — Pharmacology of Indolealkylamines (*Pharmacol. Rev.*, **6**, 425-487).
1955. ERSPAMER (V.), PAVAN (M.). — Données inédites.
1955. ERSPAMER (V.). — Osservazioni critiche sulle ipotesi concernenti il significato biologico della 5-idrossitriptamina (enteramina, serotonina) [*Medicina (Parma)*, **5**, 1-34].
1877. FOREL (A.). Der Giftapparat und die Analdrüsen der Ameisen (*Zeitschr. f. Wiss. Zool.*, **30** suppl., 28-68). — 1920. *Les Fourmis de la Suisse*. Imprimerie Coopérative, La Chaux-de-Fonds, p. 1-333. — 1922. Le monde social des Fourmis (t. II, Genève, Ed. Kundig).
- 1955 a. FUSCO (R.), TRAVE (R.), VERCELLONE (A.). — Ricerche sull'iridomirmecina, l'insetticide naturale secreto dalla *Iridomyrmex humilis* Mayr. [*La Chimica e l'Industria*, **37** (4), 251-259]. — 1955 b. La struttura dell'iridomirmecina [*La Chimica e l'Industria*, **37** (12), 958-959].
1951. GRANDI (G.). — *Introduzione allo studio dell'entomologia* Ed. Agricole, Bologna 2 vol., 1-950, 1-1332.
1954. JAKES (R.), SCHACHTER (M.). — The presence of histamine, 5-hydroxytryptamine and a potent, slow contracting substance in wasp venom [*Brit. J. Pharmac. and Chemotherapy*, **9** (1), 53-58].
1954. HASE (A.). — Die Schlupfwespen als Gifttiere. Zur Kenntnis wirtschaftlich wichtiger Tierformen II. [*Biol. Zentr.*, **44** (5), 209-243].
1906. MELANDER (A. L.), BRUES (C. T.). — The chemical nature of some Insect secretions [*Bulletin of Wisconsin Nat. Hist. Soc.*, **4** (1-2), 22-36].
1873. MOGGGRIDGE (J. T.). — *Harvesting ants and trap-door spider*. Ed. Reeve and Co., London, 1-304.
1950. NASCIMBENE (A.), PAVAN (M.). — Studi sugli antibiotici di origine animale. VIII. Ricerche su varie specie di *Formicidæ* produttrici di acido formico [*Boll. Soc. Med. Chir. Pavia*, **74** (3-4), 369-384].
1950. O'ROURKE (F. J.). — Formic acid production among the *Formicidæ* [*Annals Ent. Soc. of America*, **43** (3), 437-443].
1929. PATTON (S. W.), EVANS (M. A.). — *Insects, ticks, mites and venomous animal of medical and veterinary importance*. Ed. Grubb Ltd., Croydon, vol. 2, 1-786, 1-740.
1949. PAVAN (M.). — Ricerche sugli antibiotici di origine animale. Nota riassuntiva [*La Ricerca Scientifica*, **19** (9), 1111-1117]. — 1950. Potere insetticida della iridomirmecina e significato della sostanza nella biologia di *Iridomyrmex humilis* Mayr (*Formica argentina*) [*La Ricerca Scientifica*, **20** (12), 1853-1855]. — 1951. Sull'attività insetticida della iridomirmecina (*Mem. Soc. Ent. It.*, **30**, 107-132). — 1952 a. *Iridomyrmecina* as insecticide (*IX Int. Congr. Ent. Amsterdam*, 1951, **1**, 321-327). —

- 1952 b. Die Antibiotica tierischer Herkunft (*Zeitschr. f. Hygiene*, **134**, 136-171). — 1952 c. Sugli antibiotici di origine animale [*Boll. Ist. Sieroterapico Milanese S. Bel-fanti*, **31** (3-4), (5-6), 195-208, 232-245]. — 1955 a. Gli insetti come fonte di prodotti biologicamente attivi [*La Chimica e l'Industria*, **37** (8), 714-724]. — 1955 b. Sull'attività fitoinibente della iridomirmecina su *Lupinus albus* [*Boll. Soc. It. Biol. Sper.*, **31** (7-8), 967-969]. — 1955 c. Antagonismo della iridomirmecina verso l'effetto oncogeno della colchicina e del gammaesano su *Lupinus albus* [*Boll. Soc. It. Biol. Sper.*, **31** (7-8), 969-971]. — 1956. Studi sui Formicidæ. II. Sull'origine, significato biologico e isolamento della dendrolasina [*La Ricerca Scientifica*, **26** (1), 144-150].
1948. PAVAN (M.), NASCIBENE (A.). — Studi sugli antibiotici di origine animale. I. Su un principio antibiotico di *Iridomyrmex humilis* Mayr. [*Boll. Soc. Med. Chir. Pavia*, **72** (1-2), 193-197]. — 1948 b. Studi sugli antibiotici di origine animale. IV. Sulla presenza di sostanze antibiotiche nella testa di *Dendrolasius fuliginosus* Latr. e *Lasius bicornis affinis* Sch. [*Boll. Soc. Med. Chir. Pavia*, **72** (1-2), 207-210]. — 1948 c. Studi sugli antibiotici di origine animale. X. Nuovi risultati sulla iridomirmecina [*Boll. Soc. Med. Chir. Pavia*, **72** (1-2), 295-298]. — 1949. Studi sugli antibiotici di origine animale. IX. Sui rapporti fra estratti di Formicidæ, acido formico e alcuni formati [*Atti Soc. It. Sc. Nat.*, **88** (3-4), 136-141].
1955. PAVAN (M.), RONCHETTI (G.). — Studi sulla morfologia esterna e anatomia interna dell'operaia di *Iridomyrmex humilis* Mayr e ricerche chimiche e biologiche sulla iridomirmecina [*Atti Soc. It. Sc. Nat.*, **94** (3-4), 379-477].
1927. PAWLOWSKY (E. N.). — *Gifftiere und ihre Giftigkeit*. Ed. Fischer, Jena, 1-516.
1922. PHISALIX (M.). — *Animaux venimeux et venins*. Éd. Masson, Paris, vol. 2, 1-656, 1-864.
1956. QUILICO (A.), PIOZZI (F.), PAVAN (M.). — Sulla dendrolasina [*La Ricerca Scientifica*, **26** (1), 177-180]. — 1957. The structure of Dendrolasin [*Tetrahedron*, **1** (3), 177-185].
1954. SCHACHTER (M.), THAIN (E. M.). — Chemical and pharmacological properties of the potent, slow contracting substances (Kinin) in wasp venom [*Brit. J. Pharmacol.*, **9** (5), 352-359].
1951. STUMPER (M.-R.). — Sur la sécrétion d'acide formique par les fourmis (*C. R. Ac. Sc.*, **233**, 1144-1146). — 1952 a. Données quantitatives sur la sécrétion d'acide formique par les fourmis (*C. R. Ac. Sc.*, **234**, 149-152). — 1952 b. Sur les sécrétions odorantes de quelques fourmis (*C. R. Ac. Sc.*, **235**, 526-528). — 1953. Über Schutz- und Trutzsekrete der Ameisen [*Die Naturwissenschaften*, **40** (2), 33-34]. — 1921. Études sur les Fourmis. Recherches critiques sur l'odorat. [*Bull. Soc. Ent. Belg.*, **3** (1), 24-30]. — 1956. TRAVE (R.), PAVAN (M.). — Veleni degli insetti. Principi estratti dalla Formica *Tapinoma nigerrimum* Nyl. (*La Chimica e l'Industria*, **38**, 1015-1019).
1910. WHEELER (W. M.). — *Ants, their structure, development and behavior*. Ed. Macmillan, N. Y., 1-663.
1950. WIGGLESWORTH (V. B.). — *The principle of insect physiology*. Methuen Ltd., London, IV Ed., 1-544.
1955. PAVAN (M.), BAGGINI (A.). — Ricerche sull'attività fitoinibitrice della iridomirmecina su *Lupinus albus* [*Boll. Zool.*, **22** (2), 393-404].
1955. PAVAN (M.), VALCURONE (M. L.). — Ricerche sull'antagonismo dell'iridomirmecina verso l'attività oncogena della colchicina e del gammaesano su *Lupinus albus* [*Boll. Zool.*, **22** (2), 405-419].
1957. VALCURONE (M. L.), BAGGINI (A.). — Sulle sostanze antibatteriche di origine entomologica [*Bollettino Ist. Sieroterapico Milanese*, **36** (5-6), 283-305].



# INTERATTRACTION OLFACTIVE CHEZ *CALOTERMES FLAVICOLLIS*

## II. — POUVOIR ATTRACTIF DES NYMPHES A L'ÉGARD DES DIFFÉRENTES CASTES

par

Henri VERRON

(Laboratoire d'Évolution des Êtres organisés, Paris.)

Dans le cadre de l'analyse de l'interattraction olfactive chez *Calotermes flavicollis* (VERRON), nous présentons les résultats de l'étude du pouvoir attractif des nymphes du dernier stade à l'égard des différents individus d'une colonie de la même espèce.

### *Matériel et méthode.*

Les expériences ont été faites dans les conditions précédemment décrites (VERRON) et les mêmes précautions ont été prises à l'égard des Insectes soumis à l'expérimentation.

Rappelons que le comportement olfactif des Termites est étudié à l'aide d'un olfactomètre réalisé avec une gouttière de verre de 30 cm de long sur 3 cm de diamètre fermée dans sa longueur par une toile métallique très fine et bouchée aux extrémités par une membrane de caoutchouc. Cette gouttière, graduée en centimètres, est posée à l'envers sur six tubes équidistants de 9 cm de haut sur 2,5 de diamètre. Ces tubes sont emplis de sable humide jusqu'à 1,5 cm du bord.

Le groupe attractif est mis dans un des tubes. Le sujet réacteur est déposé sur la toile métallique à une extrémité de la gouttière. Son comportement est observé pendant une heure, et sa position dans l'appareil est relevée toutes les 3 minutes. L'attraction est mesurée par le nombre d'arrêts que fait le sujet réacteur au-dessus de ses congénères.

La signification des mesures est appréciée statistiquement par le calcul du  $t$  de Student et par l'analyse de la variance qui donne l'indice  $F$  de Snédécour.

Dans les expériences qui vont suivre, le groupe attractif est uniquement composé de nymphes du dernier stade, c'est-à-dire d'individus présentant de longs fourreaux alaires.

Les sujets réacteurs ont été pris dans 4 castes : larves, nymphes, soldats, néoténiques. Les réacteurs nymphes ont été pris parmi deux catégories de sujets :

- d'une part : ceux qui présentent de courtes ébauches alaires ;
- d'autre part : ceux du dernier stade qui possèdent des fourreaux alaires très développés.

Les réacteurs néoténiques sont issus de larves âgées mises en élevage pendant un mois. Mâles et femelles néoténiques ont été étudiés séparément.

Le pouvoir attractif des nymphes du dernier stade a été mesuré en fonction de 4 densités différentes de groupement : 5-10-15 et 20 sujets.

Pour chaque densité de groupement et pour chaque type de réacteur, 20 expériences ont été faites (soit au total 480 expériences) en changeant le sujet réacteur à chaque expérience.

### Résultats.

TABLEAU.

RÉACTEURS.	DENSITÉS.			
	5	10	15	20
Larves .....	70	105	145	175
Nymphes (ébauches alaires) .....	80	106	143	162
Nymphes (dernier stade).....	107	113	153	144
Soldats .....		85		98
Néoténiques mâles .....	64	122	144	183
Néoténiques femelles .....	74	107	144	169

### LE SUJET RÉACTEUR EST UNE LARVE.

Les animaux utilisés sont des larves de grande taille ne présentant pas d'ébauches alaires. Il s'agit donc soit de larves âgées, soit de pseudergates.

Les résultats obtenus (tableau) montrent que l'attraction augmente avec la densité de groupement.

L'analyse de la variance inter-groupes donne un indice de Snédécour de  $F = 7,84$ . Ce chiffre, très significatif, confirme le rapport étroit existant entre l'attraction et l'importance de la source attractive.

Si l'on fait une analyse comparative des résultats, on obtient un indice  $F = 23,42$ , hautement significatif, qui indique que l'augmentation de l'attraction en fonction de la densité est linéaire.

La comparaison de ces résultats à ceux obtenus précédemment (VERRON) montre que la réactivité des larves est plus faible à l'égard des nymphes du dernier stade qu'à l'égard des représentants de leur propre caste.

## LE SUJET RÉACTEUR EST UNE NYMPHE A COURTS FOURREAUX ALAIRES.

Ce stade est caractérisé par l'apparition d'ébauches alaires peu marquées.

Les résultats (tableau), confirmés par l'analyse de la variance et l'étude de la comparaison linéaire, montrent que les nymphes de ce stade réagissent comme des larves à l'égard de leurs congénères.

Pour chaque densité, les différences entre les larves et ces nymphes ne sont pas significatives.

## LE SUJET RÉACTEUR EST UNE NYMPHE DU DERNIER STADE :

On remarque ici que, pour les densités 5 et 10 d'une part, 15 et 20 d'autre part, les résultats obtenus (tableau) ne diffèrent pas significativement.

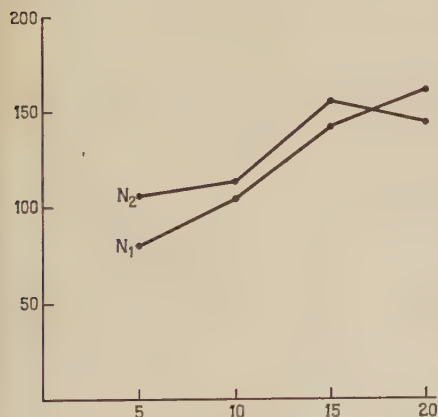


FIG. 2. — En abscisse : densité de groupement. — En ordonnée : nombre d'arrêts au-dessus du groupe stimulus.

N<sub>1</sub> : Nymphes à courts fourreaux alaires.  
— N<sub>2</sub> : Nymphes du dernier stade.

de la même manière à l'égard des larves et des individus de leur propre caste. Toutefois, leur réactivité est beaucoup plus grande à l'égard des larves pour la densité 20.

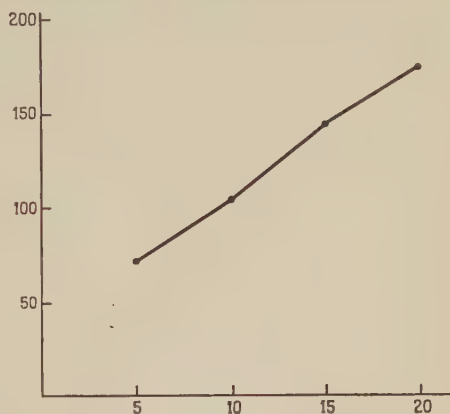


FIG. 1. — En abscisse : densité de groupement.  
— En ordonnée : nombre d'arrêts au-dessus du groupe stimulus.

Par contre, la différence est très significative entre 10 et 15. Les nymphes du dernier stade semblent donc avoir un seuil de réactivité différent de celui des larves.

— Elles réagissent :

plus que les larves pour la densité 5.

de la même manière pour les densités 10 et 15.

moins que les larves pour la densité 20.

— Elles ont une réactivité plus faible que celle des larves à l'égard des différences de densité.

Si l'on compare ces résultats aux résultats antérieurs, on voit que les nymphes du dernier stade réagissent



## LE SUJET RÉACTEUR EST UN SOLDAT :

Ce sujet ne réagit qu'à partir d'un groupe stimulus de 10 individus et sa réaction n'augmente guère quand on double la population du groupe.

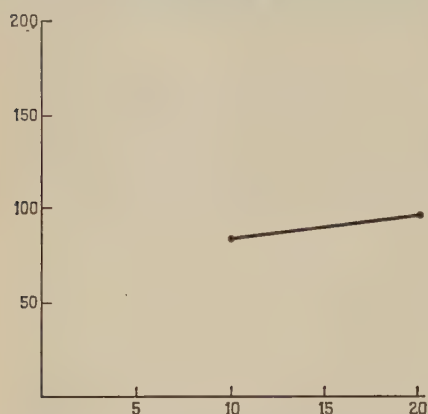


FIG. 3. — En abscisse : densité de groupement. — En ordonnée : nombre d'arrêts au-dessus du groupe stimulus.

La même constatation avait déjà été faite dans l'étude du pouvoir attractif des larves à l'égard des soldats.

La comparaison des résultats obtenus dans ces deux études montrent que les soldats réagissent plus à l'égard des nymphes du dernier stade qu'à l'égard des larves. Leur réactivité est en effet la même pour un groupe attractif de 10 nymphes et pour un groupe de 20 larves. Chez *Calotermes*, la caste des soldats est donc manifestement celle qui présente le seuil de réactivité le plus élevé et la réaction la plus faible à l'égard des autres castes de la colonie.

## LE SUJET RÉACTEUR EST UN SEXUÉ NÉOTÉNIQUE :

Le tableau ne fait pas apparaître de différences significatives entre mâles et femelles.

L'analyse de la variance inter-groupes donne  $F=7,3$ , ce qui montre de manière très significative que les sexués néoténiques sont sensibles à l'importance de la source attractive. L'étude comparative des résultats donne  $F=21,26$ . Ce chiffre, hautement significatif, indique, comme dans le cas où le sujet réacteur est une larve, que l'attraction varie linéairement avec la densité.

Pour chaque densité, les différences entre larves et sexués néoténiques ne sont pas significatives.

Si l'on compare ces résultats aux précédents, on constate que, comme pour les réacteurs larves, la réactivité des sexués néoténiques est plus faible à l'égard des nymphes du dernier stade qu'à l'égard des larves.

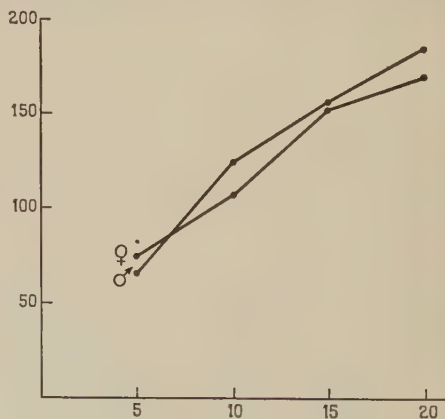


FIG. 4. — En abscisse : densité de groupement. — En ordonnée : nombre d'arrêts au-dessus du groupe stimulus.

### Résumé.

L'attraction exercée par les nymphes du dernier stade à l'égard des larves, des nymphes à courts fourreaux alaires et des néoténiques varie linéairement en fonction de l'importance du groupe attractif. Il n'y a donc pas de différence significative dans la réactivité des larves, des nymphes à courts fourreaux alaires et des néoténiques à l'égard d'un même groupe attractif.

Les nymphes du dernier stade ont un seuil de réactivité différent de celui des larves et réagissent moins aux modifications de densité du groupe attractif.

Les soldats présentent le seuil de réactivité le plus élevé.

On ne remarque pas de différence de réactivité entre les sexes chez les néoténiques.

Si l'on compare ces résultats à ceux obtenus antérieurement (VERRON), avec un groupe attractif constitué de larves, on remarque que :

— d'une manière générale, la réactivité des sujets des différentes castes (soldats mis à part) est plus faible à l'égard des nymphes du dernier stade qu'à l'égard des larves ;

— les soldats présentent, au contraire, une réactivité plus grande à l'égard des nymphes puisqu'ils répondent de la même manière à un groupe attractif de 10 nymphes et à un groupe de 20 larves.

### BIBLIOGRAPHIE

1957. VERRON (H.) — Interattraction olfactive chez *Calotermes flavicollis* (*Insectes sociaux*, 4, 3).

### Summary.

The attraction produced by last instar nymphs on larvae, nymphs with short wing pads and neotenics increases regularly with the importance of crowding.

There is no difference in response between larvae, nymphs and neotenics for a same amount of crowding.

Last instar nymphs do not show the same level of response as that exhibited by larvae; they also react less to density changes; soldiers exhibit the highest threshold of response. There does not appear to be any difference in reaction between the sexes in neotenics. These results, compared to those published formerly [attraction by larvae (1)], show that :

In most cases, the different types of individuals (soldiers excepted) do not react to last instar nymphs as well as they do to larvae.

Soldiers, however, exhibit a higher level of response towards nymphs, since they react in the same way towards 10 nymphs or 20 larvae.

### *Zusammenfassung.*

Die Anziehungskraft, die die Nymphen des letzten Stadiums auf die Larven, die Nymphen mit kurzen Flügelanlagen und die neotenischen Geschlechtstieren ausüben, variiert in linearer Abhängigkeit von der zahlenmässigen Bedeutung der attraktiven Gruppe.

Es werden keine signifikanten Unterschiede gefunden in der Wirkung einer bestimmten attraktiven Gruppe auf die Larven, die Nymphen und die neotenischen Geschlechtstieren.

Die Reaktionsschwelle der Nymphen des letzten Stadiums ist verschieden von derjenigen der Larven. Die Erstern reagieren weniger stark auf Veränderungen der Dichte der attraktiven Gruppe.

Die Soldaten weisen die höchste Reaktionsschwelle auf.

Bei den neotenischen Geschlechtstieren findet man keinen Unterschied in der Reaktion der beiden Geschlechter.

Wenn man diese Resultate mit denjenigen vergleicht, die früher mit einer aus Larven zusammengesetzten Gruppe erhalten wurden (1), dann stellt man fest :

daß im allgemeinen die Reaktion der Vertreter der verschiedenen Kasten (mit Ausnahme der Soldaten) gegenüber den Nymphen des letzten Stadiums schwächer ist, als gegenüber den Larven ;

daß dagegen die Soldaten stärker reagieren gegenüber den Nymphen, da sie auf eine attraktive Gruppe von 10 Nymphen gleich reagieren wie auf eine solche von 20 Larven.

---



# POLYETHISM IN WORKERS OF THE ANT *MYRMICA*, PART II

BY J. S. WEIR

(Formerly Carnegie Research Student, Glasgow University,  
now of the Zoology Department, University College of Rhodesia and Nyasaland,  
Salisbury, Southern Rhodesia).

## PART II.

4. CONDITIONS IN COLONIES OF <i>Myrmica rubra microgyna</i> .....	315
A.—Worker segregation (315); B.—Worker brood rearing and areal relationships of the brood mass (317); C.—Worker reaction to isolated larvae (323); D.— Worker foraging potential and survival (324); E.—Worker oviposition (327); F.— Worker sizes (330); G.—Discussion of Sections 4.A-F (331).	
5. GENERAL DISCUSSION AND CONCLUSIONS OF SECTIONS 2, 3, AND 4.....	334
SUMMARY.....	337

### 4.—CONDITIONS IN COLONIES OF *M. RUBRA MICROGYNA*

#### A. — Worker Segregation.

A typical segregation is described below. This form of segregation has been carried out, with minor variation, on numerous nests of *M. rubra*.

An early serotinal colony of *M. rubra microgyna* from the field was placed in a large container in the laboratory. Dormant larvae were being produced and were in the early third instar. The colony, containing about five hundred workers, was cultured with full food at 25°C for several days prior to segregation. It was not possible to distinguish the six melanic groups observed in the colony of *M. scabrinodis*. [Weir (1958). This will hereafter be referred to as Part I of this report, and the relevant section may also be stated.] The workers were therefore segregated by rapid removal with sucking tubes into the three ethological worker types noted previously (Part I, section 3.F) and described by Ehrhardt (1931) in *M. rubra*. These are:—

1. Workers showing high locomotor activity (here designated F-type workers),
2. Workers standing near the brood mass (here designated D-type workers),

3. Workers standing on the brood mass (here designated N-type workers).

The present part attempts to show that F-type workers are characteristic "foragers", that D-type workers are "domestics" and that N-type workers are "nurses", these three terms being used in a purely descriptive sense. Initially, these worker types are referred to as belonging to group F, D or N.

After the initial separation of the workers each group was re-separated after twenty-four hours, and only those in the same category at both separations were used experimentally, forty percent being discarded. For example, workers which at the first separation were standing near the brood mass, were placed by themselves, with ample larvae, and re-segregated after twenty-four hours. Only those workers which were then standing round the brood mass were used in the experiments, others (forty percent) which had shown a change of occupation, being discarded.

While this separation lacked the delicacy and completeness of that undertaken on *M. scabrinodis* it nevertheless achieved satisfactory segregation of the behaviour types. Melanic difference could be detected but the attempted subdivision of the three ethological types into discontinuous melanic groups was unsuccessful. Callow workers (i.e. workers produced during the current season) being recognisable by their lighter cuticular melanisation, could be completely removed from the three ethological groups, the older workers remaining showed a continuous range of melanisation from dark brown to light brown.

The callow workers were removed from the colony and cultured with some larvae. An attempt was made using the methods described above to separate callow workers into the three worker behaviour types. It was desirable, for reasons which will be detailed elsewhere, to investigate the brood rearing abilities of recently emerged workers. Three groups of callow workers were therefore segregated.

Among older workers, in order to render the ethological separation as efficient as possible, three arbitrary shades of brown were selected to represent the dominant shade of each ethal type [light brown for N-type workers, brown for D-type workers and dark brown for F-type workers], and any workers of strikingly different melanisation were discarded from the three types. About ten percent of the initial number of workers in the colony were discarded in this way.

The implications of the methods of separation used on the colony of *M. scabrinodis* have been discussed previously (Part I). Reference should be made to this discussion, bearing in mind that the present segregation has been made on the basis of:—

1. High locomotor activity as opposed to low locomotor activity.
2. Behaviour differences in the presence of larvae.
3. Segregation of arbitrary melanic groups.

**B. — Worker Brood Rearing and Areal Relationships  
of the Brood Mass.**

In the investigation of differential growth and development of larvae in groups, measurement of the degree of discriminate, biased feeding (Brian, 1951*b*) is of utmost importance (Part I, experiment 4, section 3.C). This is considered further in experiment 6 below.

TABLE 1.

	<i>N-type</i> workers.	<i>D-type</i> workers.	<i>F-type</i> workers.
Overwintered workers (Experimental) (designation ) (= Series A )	25 w 48 l	25 w 48 l	25 w 48 l
Overwintered workers (Experimental) (designation ) (= Series B )	25 w 48 l	25 w 48 l	25 w 48 l
Callow workers (Experimental) (designation ) (= Series B )	25 w 48 l	25 w 48 l	25 w 48 l

W=WORKERS; l=LARVAE.

EXPERIMENT 6. In each culture twenty-five workers of different ethal types, as described above (p. 315), were cultured with forty-eight larvae. An ethological separation of both callow workers and overwintered workers was undertaken, the nest being in a serotinal condition. The experimental design is shown in table I. The larvae used belonged in equal quantities to the first, second, and early third instars.

Nests of special construction (fig. 1) were used, providing a

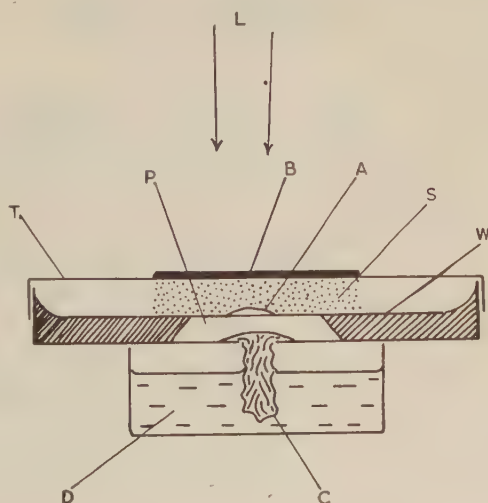
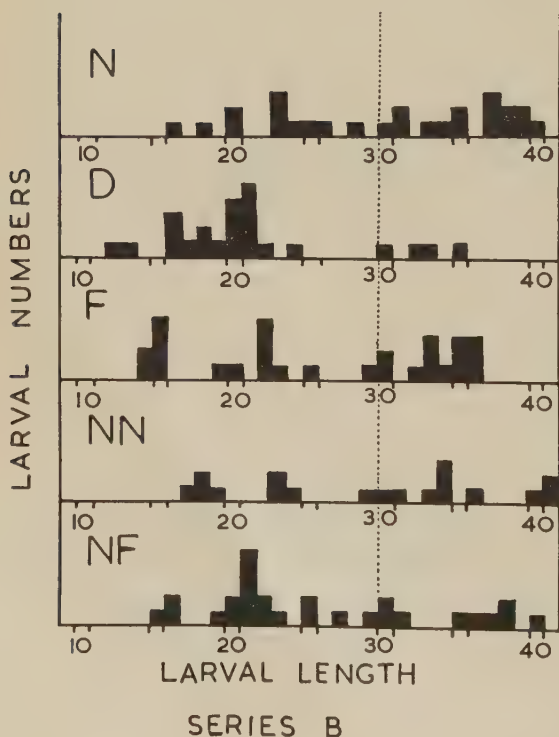
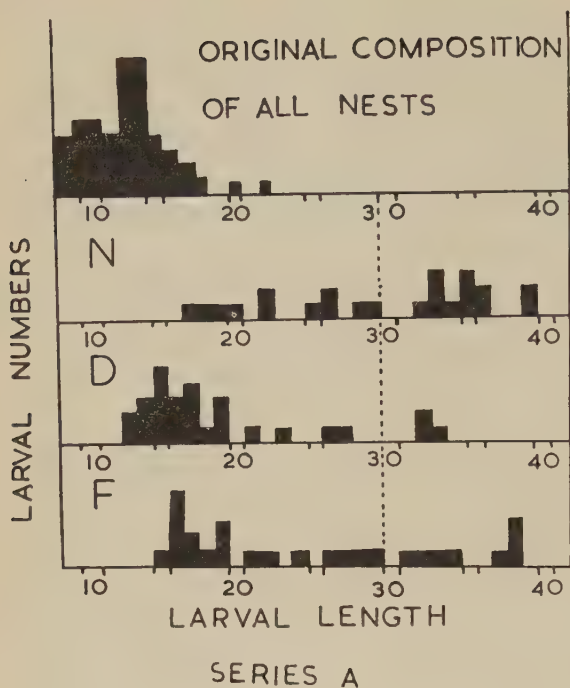


FIG. 1. — A diagrammatic section of the nest type used in these and other experiments. A, ants; B, black cover; C, cotton wool; D, water dish; L, light source; P, plaster of Paris; S, shade; T, top of glass container; W, paraffin wax.





flat surface for larval brood rearing. It is probable that the degree of biased feeding in a larval brood mass may be significantly influenced by nest structure and the resulting way in which the brood is piled by the workers. Where ten larvae are used per colony fragment (Part I, experiment 4) the problem of brood piling may not arise, but where forty-eight larvae are present standardisation of nest conditions with regard to brood piling is essential. In this connection, the significance of the nest design is as follows. The use of lights above the nest (fig. 1) for twenty-four hours after the larvae and workers are placed in the nest, allows central "fixation" of the workers and brood mass, the use of illumination then being discontinued. Experiments have shown that workers avoid:—excessive light; dry conditions; waxed surfaces.

FIG. 2. — This shows the frequency distribution of larval length in experiment 6, before and after rearing with workers of types F, D and N. The two series of nests used are shown, and included in series B are the results of larval growth in the two nests containing callow workers. (Callow nurses = NN; callow foragers = NF.) 1 unit = 0.0625 mm.

These are all combined in the nest to overcome the tendency for workers to place the larvae in corners as they do in normal plaster nests.

Central "fixation" was difficult in the case of D-type workers and centralisation was only achieved after twenty-four hours in nests containing overwintered workers of this type. After twenty-four hours continuous light treatment, and despite changes of nest, the culture of callow domestics was abandoned as intractable since larvae on piles in corners showed visible growth. This growth would affect the subsequent distribution of food among the larvae even if central fixation was then achieved. The results of the experiment would then be erroneous. The experiment was carried out at 25°C. All cultures were supplied with a full food diet.

The frequency distribution in each nest of the lengths of all larvae used was recorded initially. The results of the brood rearing analysis are shown as histograms in figure 2. All larvae over thirty units in length are undergoing development and metamorphosis. It is apparent that all worker ethal types, even in serotinal condition, are capable of producing some non-dormant larvae. There is no single ethal worker type present in the nest at this time of year which is solely responsible for the induction of larval dormancy. There are, however, significant differences ( $P = < 5 \% > 1 \%$ ) between worker types with regard to relative brood rearing success (Table 2).

TABLE 2.—THE NUMBER OF LARVAE METAMORPHOSING AFTER SIXTEEN DAYS IN EXPERIMENT 6.

	<i>N-type</i> <i>workers.</i>	<i>D-type</i> <i>workers.</i>	<i>F-type</i> <i>workers.</i>
	—	—	—
Series A.	12	3	8
Series B.	15	4	13
		Discarded	
Callows.	10	as	9
		Intractable.	

To verify the low results in D-type cultures, and confirm the initial random allocation of larvae, another experiment (7) was undertaken. Workers used in cultures of series B of experiment 6 were used again in similar nests, which were subjected to similar treatment as in experiment 6. All larvae used in experiment 7 were taken from nests of experiment 6 and all were under twenty units in length (i.e. they had not started to develop). These larvae, largely derived from D-type cultures, were randomised again, remeasured and the new frequency distribution of larval length recorded (fig. 3). Larvae in groups of twenty, with eighteen workers in each nest, showed better growth than in experiment 6. The numbers of larvae metamorphosing after twelve days for N-, D- and F-type workers respectively were 12, 2 and 9.

This is in agreement with the previous result, and shows that D-type

workers are particularly inefficient in brood rearing under these conditions. Also they show that no physiological diapause (developmental inhibition) has been induced in these larvae during the previous fourteen days.

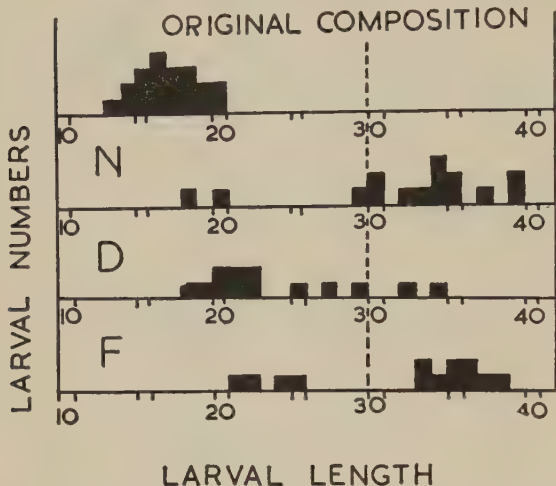


FIG. 3. — This shows the frequency distribution of larval length in experiment 7, before and after rearing with workers of types F, D and N. 1 unit = 0.0625 mm.

F cultures, shows that a large amount of biased feeding has occurred. Bias in cultures of the D group is, however, restricted to a very few larvae, although in these larvae it is almost as strongly marked as in other cultures. Heavy larval mortality in all cultures due to serotinal workers and the exigencies of nest design is shown in table 3.

TABLE 3.—% LARVAL MORTALITY IN EXPERIMENTS 6 AND 7.

	<i>N-type</i> <i>workers.</i>	<i>D-type</i> <i>workers.</i>	<i>F-type</i> <i>workers.</i>
<i>Experiment 6.</i>			
Series A.	52	42	44
Series B.	48	50	42
Callows.	62	—	44
<i>Experiment 7.</i>	25	35	35

There is a lower percentage mortality in experiment 7 due perhaps to the higher worker/larva ratio, but there is no differential mortality between worker groups. Variation in the degree of biased feeding must then be due solely to the worker ethal types.

The mechanism controlling the administration of such varying degrees of bias to the larval groups has been further investigated as follows. Repeated observations were made on the nests of series A and B of experiment 6. When the position of the brood mass had been fixed, by light,



on the plaster of Paris, the brood mass was photographed on this relatively small surface. In certain nests under certain conditions workers were standing on top of each other over the brood mass. Measurement of anything except the areas of workers and larvae then became impossible.

The experiment was performed in dim light and in darkness. Dim light was obtained by shining the light of one sixty watt lamp, six feet above the nests, onto the waxed perimeter of the arena in which the ants were kept. The ants were shaded from direct light by a circle of black paper six inches in diameter which was placed over the centre of the circular cover of the nest. A dim light penetrated to the ants. Nests in the dark were placed in large sealed boxes. A series of photographic exposures was made throughout the period of fifteen days that the experiment was in progress, and the particular series of nests undergoing each lighting treatment was varied systematically. Exposures were made with a prearranged cine-camera and the lights necessary were switched on after the camera had been started. Film then showed the conditions obtaining at the moment when the light was switched on. Nests were not exposed to this stimulus for more than twenty seconds at a time, and resulting disturbance was therefore minimised. The following factors could then be analysed statistically by the partitioning of variance (Snedecor, 1946).

1. The area occupied by workers of the three types F, D and N. [F test; P (Probability of chance occurrence)  $<0,1\%$ ].
2. The area occupied by the workers under the two different lighting conditions [F test;  $P < 5\% > 1\%$ ].
3. The area occupied by the workers as individual larval growth increased the bulk of the larval group in the course of the experiment. [F test;  $P > 5\%$ ].

A similar analysis for the corresponding factors with respect to larval area showed the following results :

1. Area occupied by larvae in nests of the three worker types F, D and N. [F test;  $P < 5\% > 2\%$ ].
2. Area occupied by larvae under the two lighting conditions. [F test;  $P > 5\%$ ].
3. Area occupied by larvae as individual larval growth increased the bulk of the larval group in the course of the experiment. [F test;  $P < 5\% > 1\%$ ].

In both sets of analyses no significance could be attributed to the first degree interaction. Second degree interaction was used as error variance.

It is apparent that the worker ethal type exerts a significant effect on both worker and larval group areas. This effect is shown graphically in

figures 4 and 5 which show the average values for both series at four successive times. The point P on the graph in figure 4 indicates that a number of workers escaped from their container at about this time, with consequent areal reduction shown. These workers were replaced by others of the same type at point Q. In both cases the F-type area is

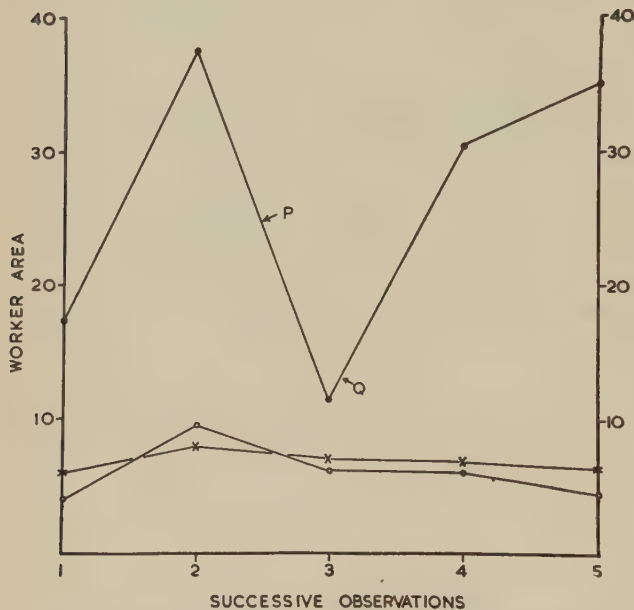


FIG. 4. — The area occupied by workers of the three types (F, D and N) at five successive observations is shown. The point P indicates the escape of a number of F-type workers from the nest. The full worker complement was restored at point Q. Worker area is measured in arbitrary units of purely relative significance. The key to the worker types is on Fig. 5.

significantly larger than the N and D areas. There is (as might be expected) a significant change in the larval area in the course of time, but there is, surprisingly, no significant interaction between worker type and time, on larval area. The effect of light is significant only with regard to the worker area. The presence of a dim light significantly reduces the "spread" of workers over the plaster of Paris and causes a build-up in the numbers of workers actually on top of the brood mass, i.e.

there is, in dim light, a significant increase in worker density on the brood mass.

While it is desirable to attempt some correlation of these areal relationships with differences in the distribution of larval bias, such correlation is not obvious. If there is no circulation of larvae in the brood mass, only those larvae lying on top will be fed. In such conditions, the extent of larval bias, i.e. the number of larvae showing growth, will be a factor of the surface area of the brood mass. While results from cultures of D-type and F-type workers are in accordance with what might be expected, the number of larvae showing growth in culture with N-type workers was large. Observation suggests that there is larval circulation in cultures of N-type workers.

Further experiments on the behaviour of these worker types while on the brood mass were unsuccessful. Observation, by mirrors, of the lower surface of the brood mass allowed accurate measurement of the

degree of larval circulation in the brood mass. The light necessary for such observations introduced the differential worker reactions noted above with the result that differing worker densities were observed on top of the brood mass. Further experiments were abandoned.

### C. — Worker Reaction to Isolated Larvae.

An attempt was made, in experiment 8, to measure the relative "attractiveness" of larvae of varying sizes to these workers. Nine larvae, three large, three medium and three small, were stuck with paraffin wax on to a sheet of filter paper, along the circumference of a circle of four inches diameter. Larvae were arranged in threes so that no two larvae of the same size were ever together. Ten workers of each ethal

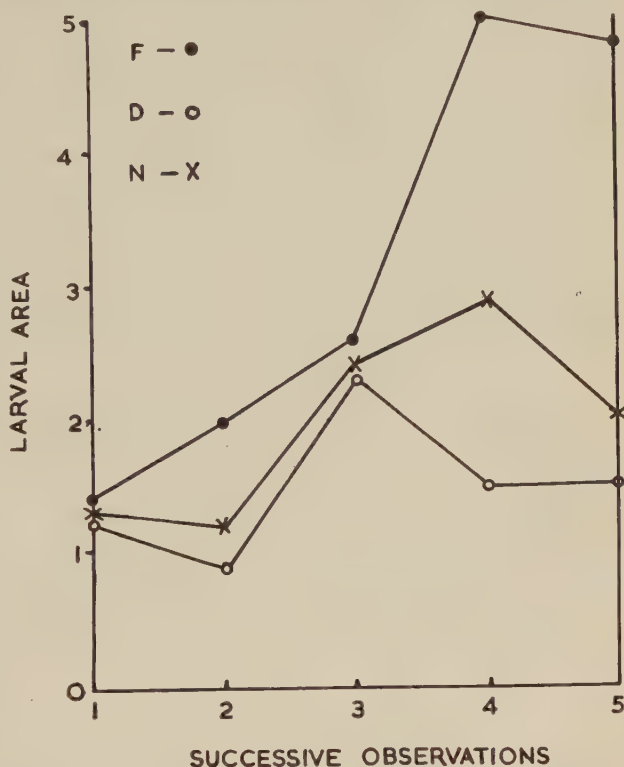


FIG. 5. — The area occupied by larvae reared by workers of the three types (F, D and N) at five successive observations is shown. Larval area is measured in arbitrary units of purely relative significance.

type from the same colony as the larvae were then released from a central container and the number "attracted" by the larvae during the following seventy-five seconds was counted.

Observation showed that several effects were being confused in this experiment. These can be detailed as follows:

1. Detection (i.e. a worker which walked over a larva might or might not detect it).
2. Collection propensity (i.e. initiation of aggregation reactions once the larva had been detected):
  - A. The worker stayed passively beside the larva.
  - B. The worker used it as a centre from which to look for other larvae.
  - C. The worker tried to pick it up and carry it away.



Behaviour of types 2A, 2B, and 2C could be observed under varying conditions if larvae were not fixed down. The fixation of larvae reduced possible incidence of some group effects, and allowed rapid observation. Confusion could result from the incidence of behaviour of type 2B. Therefore if a worker showed this behaviour it was considered to be attracted by that larva (even when looking for other larvae).

For each ethal type, three sets (each of ten workers) were used. All larvae remained alive throughout the experiment. Total results are shown in table 4. Significant differences are attributable to the three larval sizes, and to F-type workers as opposed to N- and D-type workers. Surprisingly perhaps, workers which spend most time on the brood mass are least sensitive to the presence of larvae, while workers of high locomotor activity rapidly detect such larvae. It is, however, only these highly active workers which may have previously encountered conditions in nature comparable to those in which the experiment was conducted.

TABLE 4.—TOTAL NUMBER OF WORKERS ATTRACTED BY THE LARVAE IN EXPERIMENT 8.

	<i>F-type</i> workers.	<i>D-type</i> workers.	<i>N-type</i> workers.
	—	—	—
Large larvae.	70	21	27
Medium larvae.	53	12	19
Small larvae.	21	6	0

#### *D. — Worker Foraging Potential and Survival.*

Differences in the foraging potential of the three worker ethal types are probably connected with differences in their aggressiveness or "killing power", which have been investigated in nine experiments. These will not be described in detail.

In five of these experiments, special culture tubes were used which did not contain a wet cotton wool plug. The water supply was provided by a fine tube with a cotton wool plug in the end, which siphoned water to the level of the tube. Workers could reach this plug and drink from it. Air circulation was also achieved by a fine capillary tube plugged with cotton wool. A fixed number of workers and larvae were placed in these tubes along with a fixed number of insect larvae of other kinds, and the tube sealed with a wax cork for several hours. The number of the other insect larvae killed was then found.

Results of these five experiments showed that all worker types could kill a high proportion of the *Drosophila* larvae offered. Only when excessive numbers of *Drosophila* were enclosed in the tubes could any conclusive differences be established. F-type workers then killed many more *Drosophila* larvae than were necessary for food consumption.

No immediate differences were observed in the killing of blowfly larvae (*Lucilia* and *Calliphora*) of a wide size range, between cultures of the various worker types. But if the blowfly larvae were removed after some hours in the ant nest and reared for several days, significant differential mortalities resulted (e.g. no blowfly larvae from F-type cultures survived more than twenty-four hours, while some blowfly larvae from D-type cultures and all blowfly larvae from N-type cultures survived apparently unharmed). Stings and bites on the blowfly larvae could be counted and these showed a significantly higher number of attacks by F-type workers.

The death rate of F-type workers was significantly high in these experiments, after culture for twenty-four hours with large blowfly larvae. This appeared to be due to "exhaustion" following repeated and prolonged attacks on the blowflies. This "worker exhaustion" condition was recognised by the workers being stationary for long periods, showing spasmodic twitching of legs, abdomen and head, and by what appeared to be a lack of muscular tone in legs, thorax and abdomen.

The relative survival under adverse conditions of these three types of workers was examined in experiment 9. A colony containing about 500 workers in aestival condition was separated into types F, D and N. The D group was subdivided into two sections depending on whether they resembled type F [i.e. D(F)] or type N [i.e. D(N)]. These four worker groups were then cultured in plaster of Paris nests (Brian, 1951*a*) at 25°C, without food, but with water, for thirty-four days. Dead bodies were removed each week. The original numbers in each culture, the number of survivors and the percentage survival is shown in table 5.

TABLE 5.—WORKER SURVIVAL IN EXPERIMENT 9.

...	WORKER TYPE.			
	<i>F.</i>	<i>D (F).</i>	<i>D (N).</i>	<i>N.</i>
Initial number of workers.	83	99	120	185
Number of survivors.	5	8	53	165
Percentage survival.	6 %	6.1 %	44.2 %	89.2 %

It is apparent from table 5 that the expectation of life under these conditions is high in group N, and moderate in D(N), and very low in D(F) and F. Among the possible explanation of such a result are:

1. The presence of a larger fat body in N-type workers.
2. Lower locomotor activity in N-type workers causing smaller consumption of the fat body compared with high energy utilisation of F-type workers (assuming comparable quantities of reserve food are present in both these types of worker).

It is noteworthy that this differential mortality has occurred even in the absence of insect prey, so "worker exhaustion" as described above

cannot be held responsible. Observation on these nests showed that despite higher worker numbers in the N-type culture, these workers were all grouped in the wet chamber, while F-type workers were distributed uniformly throughout the nest, and other cultures showed intermediate distributions.

Estimations of the total nitrogen content of these three worker types were made, using the micro-Kjeldahl technique of Ma and Zuazaga (1942). While significant differences were found between workers of these groups with regard to the nitrogen content of the abdomen, the full implications of these differences can only be understood by examination of individual workers. This is at present incomplete. It appears, however, that some of the seasonal differences observed in nitrogen content are related to the exhaustion of the worker fat body in early aestival condition, and the subsequent increase in the bulk of the fat body in serotinal workers. There is therefore in some workers a seasonal cycle of exhaustion and replenishment of the fat body. The results of the nitrogen analysis are shown in table 6. Only the abdomen was analysed. Table 7 shows the averaged percentage water and nitrogen compositions of six groups of workers each comprising four groups of ten workers. The result of the equivalent nitrogen estimation on twenty recently emerged workers (twenty days old at 25°C) is also shown. While percentage values are shown in table 7, the absolute values may have greater biological significance. Some of these are shown in table 6. The present work shows that there are consistent chemical differences between certain of these worker groups. The biological importance of these observations will be considered elsewhere.

TABLE 6.—THE AVERAGED VALUES IN MILLIGRAMS OF THE WET WEIGHT AND DRY WEIGHT OF THE ABDOMEN, FOR TEN WORKERS OF EACH TYPE, IN WINTER AND SUMMER.

	ÆSTIVAL WORKERS.		HEIMAL WORKERS.	
	<i>Wet weight.</i>	<i>Dry weight.</i>	<i>Wet weight.</i>	<i>Dry weight.</i>
<i>F-type workers.</i>	5.8	2.2	8.5	3.2
<i>D-type workers.</i>	6.7	2.2	8.3	3.1
<i>N-type workers.</i>	6.7	2.3	7.6	2.6
<i>Callow workers.</i>	7.5	2.1	—	—

TABLE 7.—THE % WET WEIGHT COMPOSED OF WATER AND THE % DRY WEIGHT COMPOSED OF NITROGEN, OF THE ABDOMEN.

	ÆSTIVAL WORKERS.		HEIMAL WORKERS.	
	% Water.	% Nitrogen.	% Water.	% Nitrogen.
<i>F-type workers.</i>	63.2	10.0	62.1	9.4
<i>D-type workers.</i>	67.5	9.2	62.5	8.8
<i>N-type workers.</i>	66.0	8.9	65.4	9.8
<i>Callow workers.</i>	72.5	12.9		



It should be realised that cuticular nitrogen is also estimated and may be the source of much of the nitrogen estimated. If cuticular nitrogen is a constant by comparison with the variation in nitrogen in internal organs, then the observed variation in nitrogen content may be more significant than appears here. Results as given here should however be treated with reserve since size differences between the ethal groups (as demonstrated in section 4.F below) must inevitably affect these results by differences in the quantity of cuticular nitrogen, and possibly by differences in the maximal bulk of the fat body.

Experiments have been undertaken to measure the food preferences of these three worker types throughout the year. These were unsuccessful. Accurate measurements were made over a period of days of the amount of sugar solution ingested in a series of vernal worker cultures. Feeding was sporadic, reaching a peak between the third and eighth days, and observation showed that it was largely due to individual workers in each culture. Dye marking of sugar showed that individual workers could retain and redistribute this sugar to other workers for periods of up to nine days after feeding (at 25°C). These "sugar reservoirs" may be supposed to have masked differences in the sugar consumption of the three worker types during the period of investigation.

Similar experiments on the measurement of protein consumption were still more markedly unsuccessful. Crushed blowfly (*Calliphora*) fat body was used to provide a uniform natural insect protein supply. This was largely refused by workers of all kinds, even under starvation conditions. Certain of these workers readily attacked and killed live blowfly larvae (*Calliphora*) when placed in the same containers. It seems that the crushing of the blowfly fat body rendered it much less attractive (or recognisable) to workers. It is possible that stimuli from living or recently dead insects (possibly scent or movement) are necessary before workers will feed on them.

### *E. — Worker Oviposition.*

Brian (1953) has investigated worker oviposition in *Myrmica*. He concludes that eggs are laid by all workers. The present experiments amplify Brian's observations. Three experiments are described below and will be described more fully elsewhere.

EXPERIMENT 10: This comprised three groups, each of thirty-five workers of types N, D and F. The results of weekly egg censuses (the egg input) during a period of five weeks is shown in figure 6. Type N has an egg input maximum during the second and third weeks. This maximum is greater than that of either type F or D, which achieve a maximum about the third week.

EXPERIMENT 11: This comprised four sets of cultures of each of the three worker types (F, D and N). The four consisted of two, five, ten and twenty workers. The egg input from all cultures during the first week

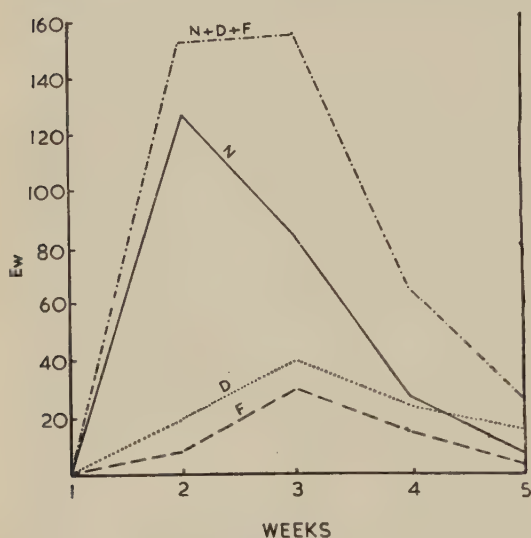


FIG. 6. — This shows the relative worker oviposition by the three worker types F, D and N. ( $E_w$  = worker oviposition). The calculated total value  $N + D + F$  is inserted.

was nil, but during the second week the egg input of cultures of N-type workers showed a regression on worker number. [ $e = 3.515w - 1.014$  where (as in Brian, 1953);  $e$  = number of eggs, and  $w$  = number of workers. Standard error of the regression coefficient being .014 eggs per worker.] Egg input during this week in cultures of types F and D was sporadic and was confined to two cultures. If 80 % efficiency of separation of the worker types is claimed, oviposition in F and D cultures is explicable on the basis of the inclusion by chance of 20 % N type workers in these cultures. If this is the case then the egg input of N-type cultures

may represent only 80 % of the maximal theoretical value.

EXPERIMENT 12: This consisted of four groups, each of four cultures, each culture containing ten workers. The workers had been hibernated at 10°C immediately prior to the experiment. Of the four cultures in each group, one consisted of F-type workers, two of D-type workers and one of N-type workers. The weekly egg input of each culture during seven weeks is shown in tables 8 and 9. Four of the five groups of cultures were subjected to various experimental treatments, the fifth acting as a control. Workers of type F showed a consistently lower egg input compared with those of type D, which in turn was lower than that of type N. These differences were apparent in spite of the effects of the treatments on both oviposition and worker survival (Weir, 1957).

Earlier results on worker oviposition in *Myrmica* (Brian, 1953) may have been affected by the lack of ethal segregation of the workers. Some variability encountered by Brian is interpretable in terms of worker polyethism. For example, in Brian's results the delay in the onset of oviposition in some cultures suggests accidental partial separation of the workers into ethal groups. Similarly, the sequence of changes in the level of egg input, observed by Brian, can be explained in terms of two successive

TABLE 8.—WORKER OVIPOSITION IN EXPERIMENT 12.

	TREATMENT.															
	I				II				III				CONTROL.			
Worker Type.	F	D	D	N	F	D	D	N	F	D	D	N	F	D	D	N
Week 1.										3	4	6				
2.									4	4	8	10				
3.							3	3	3	12	13	17		6	9	12
4.					5	24	—*	29	2	14	12	27	25	32	33	33
5.	17	13			7	23	—	20		21	17	34	13	27	23	30
6.		9	16		6	13	—	21	5	9	14	30	17	16	9	21
7.					2	**	—	5		7	15	12	14			6
Total egg production.	26	29			20	60	3	78	14	70	83	136	69	81	74	102
Worker survival.	8	6	4	3	3	0	—	5	7	5	9	6	9	7	7	9

\* Culture accidentally destroyed.  
 \*\* No workers alive after this week.

peaks of egg production. The first, derived from N-type workers merging into a second and less abrupt peak caused by F and D type workers. The greater rapidity of these changes in cultures of isolated worker types may

TABLE 9.—EGG PRODUCTION IN EXPERIMENT 12 DISREGARDING TREATMENT.

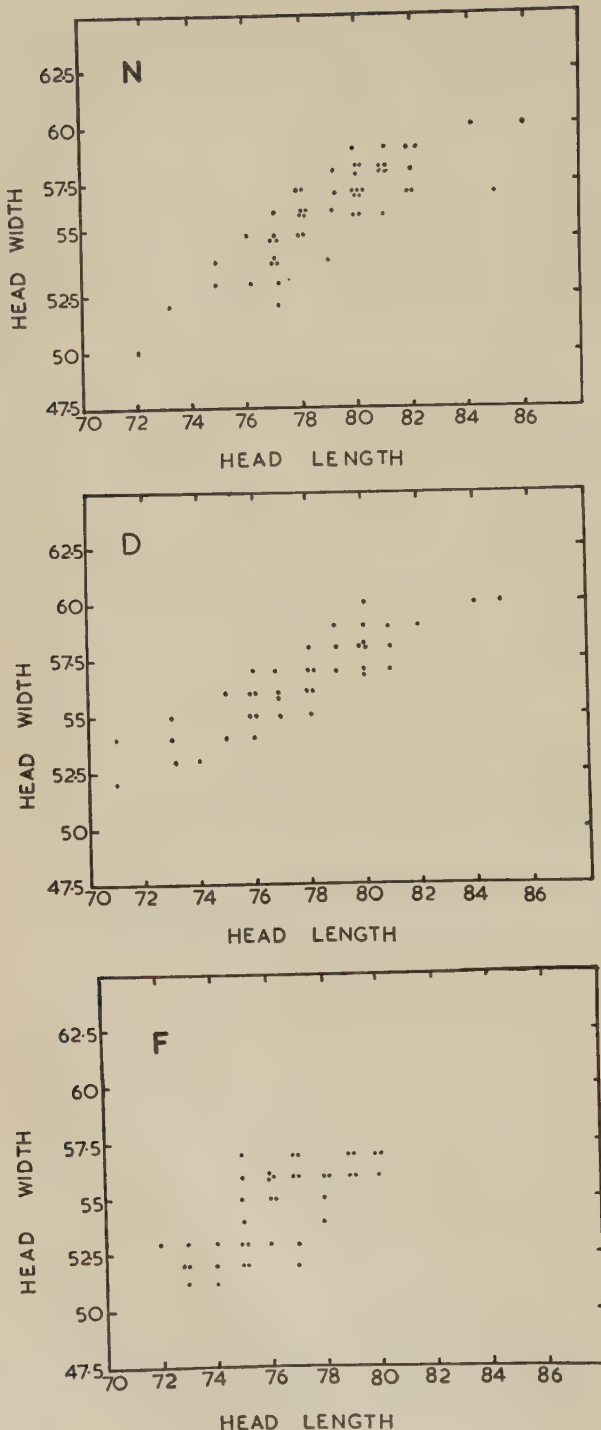
	WORKER TYPE.			
	F	D	D	N
Week 1.	—	3	4	6
2.	4	4	8	10
3.	3	18	25	32
4.	32	70	45	89
5.	20	88	53	84
6.	28	47	39	72
7.	16	7	15	23
Totals.	103	237	189*	316

\* One culture lost.

be attributed to the use of a different subspecies *M. rubra microgyna*, as opposed to *M. rubra macrogyna* (or to the systematic fragmentation in the present experiments of the integrated worker components of the colony).

Conclusions with regard to polyethism and worker oviposition are:





a. All experiments show differences between the three worker types, nurses having higher egg inputs than domestics, which may have higher inputs than foragers.

b. Differences in the time of production of eggs by these worker types show a high initial egg input peak of the N-type workers, followed by the lower egg input peak of the other types.

#### F. — Worker Sizes.

Measurements were made on workers of *M. rubra microgyna* from a colony in aestival condition. Workers were segregated into behaviour types F, D and N. At the time of measurement, no workers had been produced from non-dormant larvae of that season. Callow workers produced in the spring from dormant

FIG. 7. — This shows the relationship between head width and head length in overwintered workers of the three types F, D and N. I unit = 0.0154 mm. It is apparent that the sample of F-type workers contains few large individuals

brood were segregated from overwintered workers and removed. Complete segregation into ethal types of all workers being impossible, only a sample from each segregate was measured. Sample sizes were:—50 N-type workers; 40 D-type workers and 40 F-type workers.

The measurements made were those of head length and head width (1 and 2, as for *Myrmica scabrinodis*, part I, section 3.E). It is probable, from the results of the measurements of *M. scabrinodis* that head width is an adequate measure of total worker size. These measurements are shown in figure 7.

The following conclusions can be drawn.

- a. There is considerable size variation between members of one colony.
- b. There is no detectable allometry.
- c. There is considerable overlap of the frequency distribution of head size of the overwintered workers, but differences are apparent.
- d. In the overwintered worker groups, the frequency distribution of head size of N and D workers is identical. F-type workers only occur throughout part of this size range, and do not include large individuals.

#### G. — Discussion of Section 4.A-F.

It is concluded, from the above observations on conditions in colonies of *Myrmica rubra microgyna* that the segregation of workers into three behaviour types is justified. Diagnostic differences between these three types of *Myrmica rubra microgyna* (F, D and N) may be characterised as follows:—

*F-type Workers.* These show: 1. High locomotor activity in the original segregation.—2. Strong cuticular melanisation.—3. Large areal spread of groups round the brood mass when by themselves.—4. High efficiency in killing blowfly larvae.—5. High mortality after culture with blowfly larvae.—6. High mortality during starvation.—7. High efficiency in the detection of isolated larvae of all sizes.—8. Low rate of egg production.

*D-type Workers.*—These show: 1. Low locomotor activity, standing near the brood mass in the original segregation.—2. Moderate-strong cuticular melanisation.—3. Small areal spread of a uniform group of workers round a brood mass under standardised conditions.—4. Moderate efficiency in killing blowfly larvae.—5. Low mortality after culture with blowfly larvae.—6. Moderate mortality during starvation.—7. Moderate efficiency in the detection of isolated larvae of large and medium sizes, but inefficient detection of small larvae.—8. Moderate-low rate of egg production.

*N-type Workers.*—These show: 1. Low locomotor activity, standing

on the brood mass in the original segregation.—2. Moderate cuticular melanisation.—3. Small areal spread of a uniform group of workers round a brood mass under standardised conditions.—4. No efficiency in killing blowfly larvae.—5. No mortality after culture with blowfly larvae.—6. Low mortality during starvation.—7. Moderate efficiency in the detection of isolated larvae of large and medium sizes, but inefficient detection of small larvae.—8. High rate of egg production.

Comparison of these results shows that on the basis of these eight differences alone, the separation of workers into types F, D and N is justified. By analogy with the colony of *Myrmica scabrinodis* described earlier, types F, D and N may be designated “foragers”, “domestics” and “nurses” respectively. The relationship of these groups to the melanic groups demonstrated in *M. scabrinodis* is discussed below (p. 334).

In addition to the eight differing aspects of the worker types enumerated above, there are other diagnostic features. Differences in queen-rearing efficiency between these three worker types will be described elsewhere (N-type workers can be distinguished from the other types on this basis). The implications of worker size differences, and worker brood rearing differences are discussed below (p. 333). Differences in nitrogenous composition of these three types have been shown to exist, these are not considered further in this paper.

Differences in the brood rearing success of the three types are examined in section 4.B, experiment 6, above. It is shown that differences in the extent and distribution of biased feeding may vary with the surface area of the brood mass. The larval area in F-type cultures is large since the larvae are not piled. Many larvae show growth increases. Thus the high foraging potential of F-type workers allied to their tendency to spread the brood mass under these conditions, may cause the widespread larval growth observed.

Low foraging potential allied to brood piling in D-type workers may cause the opposite effect. Larval groups reared by D-type workers show that feeding is restricted to a very few larvae.

The same condition apparently prevails in cultures of N-type workers which also show low foraging potential combined with a tendency to pile the brood. The extensive larval growth shown by this group (and comparable to that shown by F-type workers) can be explained by the following observations:—

1. In certain laboratory nests, circulation of the larvae in the brood mass by the workers has been observed. The factors controlling brood circulation are unknown. Such circulation results in the incessant movement of larvae from one portion of the brood mass to another so no single larva may be exposed for excessively long periods on top of the brood mass. The distribution of bias is then not controlled by the surface area of the brood mass.
2. While workers of type N show low foraging potentials similar



to those of type D, they have a much higher rate of egg production than D-type workers. There is therefore ample larval food available in N-type worker cultures, but it may have differing qualitative effects compared with the F-type larval food. These might not be detectable in this experiment. [Experiments showing the importance of eggs as food for larvae will be described elsewhere].

The apparently surprising result (section 4.C) that F-type workers were more "attracted" to individual larvae than workers of types D or N is comprehensible if the experimental conditions are considered. Workers were subjected to stimulation both by removal from a culture tube, liberation, and the presence of a bright light. Also, in the case of N and perhaps D-type workers, there was no nest scent in the new environment. F-type workers, with higher locomotor activity, may well have been repeatedly exposed to these and similar extra-nidal stimuli, and so might be partially conditioned to ignore them. Also it may be suggested that F-type workers, possibly three years old, may be more sensitive to the presence of individual larvae. Perhaps also, one of their normal duties is the recovery and transport of individual larvae in the nest.

The significance of size differences between workers of these three ethal types lies in the possibility that size may, to some extent, control the functional preference of the worker. Such a possibility was demonstrated in the colony of *M. scabrinodis* (Part I, sections 3.E,F). The size analysis of samples of workers from a colony of *M. rubra microgyna* (section 4.F) shows that F-type workers cover only part of the size range of N and D-type workers, the average size of F-type workers being smaller. Among the possible explanations of this result are:—

- [1] There has been experimental discrimination of small workers for measurement in the F-sample for unknown reasons.
- [2] This size range difference is demonstrable among all workers in the colony. If this is the case the possible explanations can be further analysed as follows:—
  - i) There is differential mortality of large workers prior to or during the time of foraging.
  - ii) No large workers become foragers.
  - iii) Assuming a change of job-preference with age, initial worker size differences are accompanied by differences in the rate of change of job-preference, and, in this species, the duration of worker life is such that no large workers (with slow changes of job-preference) live long enough to become foragers.

## 5.—GENERAL DISCUSSION AND CONCLUSIONS OF SECTIONS 2, 3 (PART I) AND SECTION 4 (PART II)

The experimental work undertaken in these sections shows conclusively that there is some degree of division of worker labour in both *Myrmica scabrinodis* and *Myrmica rubra microgyna*. This system is best analysed on the basis of three worker occupations.

### 1.—*Nurses*

[Workers on the brood mass.]  
[           N-type workers           ]

### 2.—*Domestics*

[Workers standing near the brood mass.]  
[   Workers preferring to build nests   ]  
[           D-type workers           ]

### 3.—*Foragers*

[Workers showing high locomotor activity]  
[           F-type workers           ]

These are approximately the same categories as Ehrhardt (1931) distinguished in colonies of *M. rubra*. [The species used by Ehrhardt (1931) may not have been *Myrmica rubra* as investigated by Brian and Brian (1949) and here used by the present author, but may have been *Myrmica laevinodis* (as revised by Brian and Brian, 1949)].

Detailed comparison of the conditions observed in the two species *M. scabrinodis* and *M. rubra* is difficult because of the different basis of worker separation employed in each species. The degree of worker segregation achieved in *M. rubra* (Ehrhardt, 1931) and in *M. rubra microgyna* (Part II, section 4 above) is approximately comparable, but many experimental consequences of this worker separation have been demonstrated in *M. rubra microgyna*. This contrasts with Ehrhardt's work which was based largely on the observation of individual workers over long periods of time.

Worker segregation into behaviour types of an entire colony of this genus has not previously been achieved, and the segregation of the colony of *M. scabrinodis* (Part I, section 3) has allowed more detailed investigation of the worker age-function relationships than has hitherto been possible. The results of this analysis show the existence in *M. scabrinodis* of a dynamic worker-job-preference mechanism comparable to that known to exist in *Apis*. The implications of this mechanism in *M. scabrinodis* have been fully discussed in Part I, section 3.F.

There remains the difficulty of reconciliation of the results achieved in these two species. The occurrence of detectable melanic differences

in *M. scabrinodis* facilitated rapid differentiation of the types visually, and thus complete segregation, while neither was possible in *M. rubra*. This has resulted in a different experimental approach to these two species. Only in *M. scabrinodis* have dynamic worker-job-preferences been experimentally confirmed. Nevertheless, the fact that it was possible to segregate *M. rubra* colonies shows that this mechanism, with its plasticity of worker function, exists also in *M. rubra*.

It is necessary therefore to extrapolate those conclusions which were derived from experiments on *M. scabrinodis* and apply them to *M. rubra*. It seems probable that the colour-age-activity-behaviour separation carried out on *M. scabrinodis* cannot be applied to *M. rubra*, largely because of the lesser degree of melanisation shown by workers of *M. rubra*. The possibility remains of minor variations between the polyethal worker systems of these two species. In any case, the fundamentals of the dynamic worker-job-preference system do not appear to vary significantly between the two species.

In both species there is some evidence that worker size may affect worker-job-preference. The variation in average worker size of the two annual brood batches may therefore result in quantitative seasonal changes in the types of work undertaken in the colony, although the dynamic nature of the system may well entirely mask such effects.

The theoretical implications of this dynamic system on myrmicine sociology have been examined partially in section 3.F, Part I, and will be considered elsewhere in greater detail.

The primary aim of this investigation, which was to examine the variation in worker activity and the relationship of this variation to differences in worker brood rearing capacity, has been only partially successful. Experimental conditions masked the relevant effects in sections 3.B,C, Part I. Quantitative effects on the distribution of bias among groups of larvae were, however, forthcoming both from the results of section 3.C, Part I and from section 4.B, Part II. These show that D-type workers of *M. rubra* are consistently unsuccessful in brood rearing, and tend to produce a few large developing larvae from any one group, this effect being due perhaps to both low oviposition rates and brood piling without circulation (the latter possibly a laboratory artifact reflecting the nest constructing tendencies of this group). Both F- and D-type workers produce a wide range of larvae of all sizes.

In *M. scabrinodis* the most obvious differences were due to the bad larval growth in cultures which contained only nurses. It appears that the presence of a small proportion of workers of other melanic groups produces the best results.

In both species the brood rearing success of the colony will be affected by changes in the proportions of workers of these types in the colony, e.g. the presence of numerous domestics among workers on the brood will reduce the efficiency of the nurses by dilution, by inefficient response to larval signalling, and, at least in laboratory colonies, by positive effects,



such as brood piling. Such changes in colony composition may well be seasonal, and occur in nature. Quantitative estimation of the seasonal variation, in natural colonies, of these ethal worker types has not been undertaken.

The worker-job-preference structure here demonstrated in *M. rubra* and *M. scabrinodis* may be compared (as a system of functional dominance) with the dominance order relationships described by Pardi (1948) on *Polistes*, Free (1955) on *Bombus*, and those reviewed by Ribbands (1953) on *Apis*.

Research on *Polistes* and *Apis* has demonstrated the possession of a unidirectional dominance system among individuals of the colony. In this system, dominance is associated most strongly with the queen, next with egg-laying and brood-tending workers, and finally, with workers which stay away from, or are driven away from, the brood mass, i.e. foragers.

In *Myrmica*, the present work shows that in addition to a similar queen and brood centred dominance system, operating outwards from the brood chamber, there is also a dominance system operating in the reverse direction. It has been shown that, in the absence of nurses, brood rearing is undertaken by foragers although with less efficiency. It has also been shown that, in the absence of foragers, nurses will, to a small extent, start foraging. Neither of these groups is completely efficient in the "wrong" job, but neither is completely inefficient. On the basis of these results, social dominance in *Myrmica* cannot be separated from spatial effects, i.e. nurses are dominant to foragers when on the brood mass, but foragers are dominant to nurses when far away from the influence of the brood mass.

It follows that the addition of foragers to a colony fragment composed of larvae and nurses alone, will suppress the locomotor activity of the nurses (Part I, section 3); and similarly, the addition of nurses to a colony fragment composed of larvae and foragers alone will result in increased foraging, as foragers will leave the brood mass (Part I).

In such a social system where dominance effects can be associated with locality, the importance of a relatively fixed position for the brood mass is apparent. Nevertheless, even in the absence of a brood mass or queen, a synthetic colony composed only of nurses and foragers will not disintegrate. The nurses tend to aggregate in the "wet" chamber of the nest, while foragers spread evenly throughout all chambers and show no tendency to aggregation (Part II, p. 326). This concentration of social tendencies in young nurse individuals may be compared with observations on old workers of *Apis mellifera*, which sometimes leave the colony completely before they die. Older individuals are in both cases tending to non-social behaviour.

In this connection, it may be noted that protein foraging in a composite colony fragment, in the laboratory, is not necessarily limited to the needs of the colony fragment. For instance, heaps of killed *Drosophila* larvae

(the protein food supplied to laboratory colonies) may be deposited beside the brood mass (Part I). The older individuals (foragers) have behaved in a way quantitatively unrelated to the needs of the colony.

The problem of functional efficiency coupled with locality dominance may then be considered as competition for worker energy throughout the life of the individual between, first, the social attributes (spatially fixed and localised within the confines of the colony) of the young workers, and second, the individualistic attributes (spatially unrestricted) in old workers. In this competition, the initially dominant social attributes of the young individuals steadily lose, until the old individual becomes partially anti-social and may leave the colony for long periods of time, the attributes of the solitary individual then being dominant.

### *Résumé de la seconde partie.*

L'étude expérimentale des variations de comportement et d'activité locomotrice ouvrière chez *Myrmica rubra microgyna* a donné les résultats suivants.

1. Comme pour *M. scabrinodis* on reconnaît trois groupes éthologiques. On relève les différences entre ces trois groupes au point de vue de l'activité locomotrice, du comportement, de l'élevage du couvain, de la reconnaissance de larves, de la puissance meurtrière de la survivance, de la constitution chimique, de la ponte et peut-être aussi de la taille.
2. On démontre la souplesse éthologique ouvrière en relevant des apparences d'organisation dynamique ouvrière — tâche préférentielle malgré l'absence d'une discontinuité de mélanisme entre les tranches ouvrières de l'espèce.

On rapproche les travaux entrepris sur *M. scabrinodis* et sur *M. rubra microgyna* en indiquant leur portée corrélatrice aussi bien que leurs rapports avec d'autres travaux de l'auteur sur l'efficacité de l'élevage des couvées, et on discute ce qui en résulte, en fonction des travaux antérieurs sur les rapports de dominance chez d'autres insectes sociaux.

### *Summary of Part II.*

Variation in worker locomotor activity and worker behaviour in *Myrmica rubra microgyna* has been experimentally investigated, with the following results.

1. Three worker behaviour groups are recognised as in *M. scabrinodis*. Differences between these three groups in locomotor activity,

behaviour, brood rearing, larval detection, killing power, survival, chemical constitution, oviposition, and possibly size, have been described.

2. Worker ethological plasticity has been demonstrated and aspects of a dynamic worker-job-preference organisation are detectable, despite the absence of discontinuity of melanisation between worker age groups in this species.

The significance of the observations of the present author on *M. scabrinodis* are correlated with those on *M. rubra microgyna*. The relationship of these observations to other work by the present author on brood rearing efficiency is indicated, and their implications in respect of earlier work on dominance relationships in other social insects is discussed.

### *Resumen. — Sección II.*

De forma experimental, se ha investigado la variación en la locomoción y comportamiento de la trabajadora *Myrmica rubra microgyna*, con el siguiente resultado:

1. Como en la *M. scabrinodis*, se reconocen tres grupos etológicos de trabajadoras.

Se describen las diferencias entre estos tres grupos como ser en su actividad locomotora, comportamiento, detección larval, poder destructor, el sobrevivir constitución química cuidado de su cría, colocación de huevos y posiblemente su tamaño.

2. Se ha demostrado la plasticidad etológica de la trabajadora y se descubre un aspecto dinámico en la preferencia de la trabajadora por ciertos labores y su organización, no obstante la ausencia de la discontinuación de melanización entre las distintas edades de las trabajadoras de esta especie.

El significado de estas observaciones del autor sobre *M. scabrinodis* se relaciona con aquellas sobre *M. rubra microgyna*. Asimismo, se indica que estas observaciones se relacionan con otro trabajo del autor sobre la eficiencia de cría. Se discute también su implicación con respecto a previo trabajo concerniente a relaciones dominantes en otros insectos sociales.

### REFERENCES

- BRIAN M. V. (1951 *a*). Ant culture for laboratory experiment (*Ent. mon. Mag.*, 87, 134-36).  
 BRIAN M. V. (1951 *b*). Caste determination in a Myrmicine ant (*Experientia*, 7, 182).  
 BRIAN M. V. (1953). Oviposition by workers of the ant *Myrmica* (*Physiol. comp.*, 3, 25-36).



- BRIAN M. V. & BRIAN A. D. (1949). Observations on the taxonomy of the ants *Myrmica rubra* L. and *M. lævinodis* Nylander (Hymenoptera: Formicidæ) (*Trans. R. ent. Soc. Lond.*, 100, 393-409).
- EHRRHARDT S. (1931). Ueber Arbeitsteilung bei *Myrmica*- und Messor-arten (*Z. Morph. Okol. Tiere*, 20, 755-812).
- FREE J. B. (1955). The division of labour within bumblebee colonies (*Insectes sociaux*, 2, 195-212).
- MA T. S. & ZUAZAGA G. (1942). Micro-Kjeldahl determination of nitrogen (*Industrial and Engineering Chemistry*, 14, 280-282).
- PARDI L. (1948). Dominance order in *Polistes* wasps (*Physiol. Zool.*, 21, 1-13).
- RIBBANDS R. (1953). *The behaviour and social life of honeybees*, London.
- SNEDECOR G. W. (1946). *Statistical Methods*, 4th Edition, Iowa.
- WEIR J. S. (1957). Effect of anæsthetics on workers of the ant *Myrmica* (*J. exp. Biol.*, 34, 464-468).
- WEIR J. S. (1958). Polyethism in workers of the ant *Myrmica*. I. (*Insectes sociaux*, 5, 97-128).
-



## NOUVELLES DE L'UNION





## NOUVELLES DE L'UNION

---

### *Communiqué.*

« Nous rappelons à nos lecteurs que le XI<sup>e</sup> Congrès International d'Entomologie aura lieu du 17 au 25 août 1960, à Vienne. Les participants qui n'auraient pas reçu notre circulaire sont priés de solliciter auprès du Secrétariat du Congrès, Vienne I, Naturhistorisches Museum, Burgring 7, des renseignements détaillés en nous communiquant leur adresse moyennant carte postale. »

### *Modification à la liste des membres.*

*L'adresse exacte de M. Hrdy est la suivante :*

HRDY (I.) Dr., Institut d'entomologie de l'Académie des Sciences, Viničná 7, Praha 2, Tchécoslovaquie.

Intérêt : **Isoptera.**

### COMPTE RENDU DE LA RÉUNION DE LA SECTION FRANÇAISE (15 mars 1958)

Une réunion de la section française de l'U. I. E. I. S. s'est tenue le 15 mars 1958 à 17 heures au Laboratoire d'Évolution des Êtres Organisés, à Paris, avec l'ordre du jour suivant :

Situation générale de l'Union. — Publication des comptes rendus du Congrès de juillet 1957. — Communication scientifique : « Structure des Cellules Royales chez les Abeilles », par Maurice Vuillaume. — Questions diverses.

Étaient présents : M. GRASSÉ, Président ; M. RICHARD, Secrétaire ; M<sup>lle</sup> CLÉMENT, Trésorière.

M<sup>me</sup> BAZIRE, M. BUSNEL, MM. CHAUVIN, DARCHEN, DELEURANCE, GERVET, KUTTAMATHIATHU, LECOMTE, LOUVEAUX, NOIROT, REMAUDIÈRE, VERRON.

Excusés : MM. DE FEYTAUD, LAVIE, MOREAUX, WITTOUCK.

I. M. GRASSÉ et M. RICHARD exposent aux présents les résultats de leur travail depuis le congrès de juillet 1957.

— De graves difficultés financières causent des soucis au Bureau de l'Union. En particulier, les frais d'édition augmentent et il devient difficile de combler le déficit du Bulletin avec les seules subventions françaises déjà acquises. Ces difficultés ont retardé jusqu'à maintenant en particulier la mise sous presse des comptes rendus du Congrès.

— Le Secrétaire a envoyé aux Présidents de section nationale une lettre circulaire dans laquelle il demandait à chaque section de lui faire parvenir ses suggestions quant aux problèmes ci-dessous :

- 1° réduction des frais du Bulletin ;
- 2° doublement du nombre des abonnés ;
- 3° obtention de subventions de divers pays ;
- 4° augmentation du prix de l'abonnement.

Le Bureau proposait en particulier de remplacer le tiré-à-part « Nouvelles de l'Union » par un Bulletin ronéotypé semestriel adressé directement à tous les membres à jour de leur cotisation annuelle. Le tiré-à-part suppose, en effet, des frais supplémentaires d'impression, de couverture, de brochage, d'encartage, etc., qui grèvent le budget de l'Union.

A la date du 15 mars, le Secrétaire a reçu des réponses très détaillées du Professeur MICHENER et du Professeur SAKAGAMI. Tous deux se déclarent contre l'augmentation brutale immédiate du prix de l'abonnement au Bulletin. Par contre, le Professeur MICHENER pense que l'on pourrait peut-être augmenter ce prix pour les bibliothèques et laboratoires. Il pense également qu'on pourrait laisser à la charge des auteurs toutes les illustrations des textes. Il semble partout difficile de doubler rapidement le nombre des abonnés, toutefois un effort en ce sens sera fait en Amérique et au Japon comme en France. M. MICHENER comme M. SAKAGAMI sont d'accord avec la proposition de remplacement des « Nouvelles de l'Union » par un Bulletin ronéotypé. M. SAKAGAMI propose en outre, pour réduire les frais du Bulletin, de supprimer la couverture des tirés-à-part et de diminuer la qualité du papier (la section française tient, au contraire, à conserver au Bulletin sa présentation). En ce qui concerne les subventions, M. MICHENER propose de demander d'abord aux pays n'ayant fourni aucune aide de participer plus activement au soutien de notre Bulletin ; M. SAKAGAMI propose une discussion à ce sujet avec M. UCHIDA, qui sera à Paris au cours de l'été.

— Le Bureau tiendra compte de toutes ces suggestions et poursuivra ses efforts pour faire vivre et pour améliorer sans cesse le Bulletin.

— En ce qui concerne le prochain Congrès, M. GRASSÉ a reçu de M. MICHENER une lettre faisant suite aux propositions du Comité Directeur de juillet 1957. M. MICHENER pense, après discussion avec ses Collègues américains, qu'il sera difficile, pour de multiples raisons, d'organiser un Congrès aux États-Unis ; l'une des plus graves raisons serait la difficulté des Collègues européens de venir très nombreux. Il pense donc qu'il vaut mieux organiser le prochain Congrès en Europe — M. RICHARD

a donc écrit au Professeur JUCCI ; celui-ci, tout en regrettant la position des Collègues américains, doit étudier avec la section italienne les possibilités d'organisation du Congrès de Rome. Des informations ultérieures seront communiquées.

II. Les comptes rendus du Congrès de juillet 1957 sont actuellement prêts à être imprimés ; le secrétaire attend encore la décision du C. N. R. S. concernant la subvention demandée. Très probablement l'impression pourra commencer bientôt. Elle restera indépendante de la parution normale du Bulletin régulier.

III. M. VUILLAUME expose les derniers résultats de ses recherches sur la structure des Cellules Royales chez les Abeilles. Sa communication est suivie d'une discussion à laquelle participent tous les présents sous la direction de M. GRASSÉ.

La séance est levée à 18 h. 45.

---



---

*Printed in France.*

*Le Gérant :* GEORGES MASSON.

---

Dépôt légal 1958 - 3<sup>e</sup> trimestre - N<sup>o</sup> d'ordre : 2942 - MASSON et C<sup>ie</sup>, éditeurs, Paris.

---

Imprimé par l'Imp. CRÉTÉ Paris, Corbeil-Essonnes.  
Dépôt légal 1958 - 3<sup>e</sup> trimestre - N<sup>o</sup> d'ordre 9438.

## NOTES POUR LES AUTEURS

---

- 1° *Insectes sociaux* publie des mémoires originaux, des notes ou des revues concernant les problèmes relatifs aux insectes sociaux.
  - 2° Les auteurs reçoivent gratuitement 50 tirés à part.
  - 3° Les manuscrits doivent être adressés à l'un des membres du Comité de rédaction.
  - 4° Les textes remis pour l'impression doivent être dactylographiés. Leur forme sera considérée comme définitive, et leur étendue ne pourra pas dépasser 20 pages (28 lignes de 67 caractères par page) dactylographiées, illustration comprise.
  - 5° Le secrétaire se réserve le droit de demander la suppression des figures dont le nombre serait jugé excessif. Les figures au trait sont à la charge de la revue. Les planches, les photographies sont à la charge des auteurs, à l'exception de celles que le secrétaire jugerait pouvoir prendre au compte de la revue. Les documents doivent être fournis prêts à cliquer.
  - 6° Les légendes des figures doivent être indépendantes des documents d'illustration.
  - 7° Chaque article doit être accompagné d'un sommaire qui en résume les points essentiels. Il sera joint une traduction de ce sommaire en deux autres langues.
  - 8° La disposition de la bibliographie doit être conforme aux règles suivantes de présentation : Date. Nom (prénom). — Titre de l'article (titre du périodique. Année. Numéro du tome, pages de début et de fin de l'article).
  - 9° Les épreuves sont adressées aux auteurs pour correction. Elles doivent être retournées **SANS DÉLAI** au secrétaire : G. Richard, Laboratoire de Biologie Animale, Faculté des Sciences, RENNES (I-et-V.) — France.
- 

## ÉDITIONS DU CENTRE NATIONAL DE LA RECHERCHE SCIENTIFIQUE

---

### PUBLICATIONS PÉRIODIQUES

**LE BULLETIN SIGNALÉTIQUE.** — Le Centre de Documentation du C. N. R. S. publie un « Bulletin Signalétique » dans lequel sont signalés par de courts extraits classés par matières tous les travaux scientifiques, techniques et philosophiques publiés dans le monde entier.

2° partie (biologie, physiologie, zoologie, agriculture).

France : 6 500 francs. Étranger : 7 500 francs.

*Tirage à part, 2° partie, Section XI (biologie animale, génétique, biologie végétale).*

France : 3 650 francs. Étranger : 4 050 francs.

Abonnement au Centre de Documentation du C. N. R. S., 16, rue Pierre-Curie, Paris (V<sup>e</sup>). C. C. P. Paris 9131-62. Tél. : DANton 87-20.

**ARCHIVES DE ZOOLOGIE EXPÉRIMENTALE ET GÉNÉRALE.** — Revue trimestrielle publiée sous les auspices du « Comité des Archives de Zoologie expérimentale et générale ».

Prix de l'abonnement : France : 4 500 francs. Étranger : 5 000 francs.

Vente : Presses de la Cité, 116, rue du Bac, Paris (VI<sup>e</sup>).

**JOURNAL DES RECHERCHES DU C. N. R. S.** — Publication trimestrielle.

Abonnement annuel : France : 1 200 francs. Étranger : 1 500 francs.

Vente : Laboratoires de Bellevue, 1, place Aristide-Briand, Bellevue.



23-06-2023

23-06-2023

**M**  
**&**  
**ie**